

*REINFORCEMENT VALUE AND SUBSTITUTABILITY OF SUCROSE AND WHEEL RUNNING:
IMPLICATIONS FOR ACTIVITY ANOREXIA*

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Choice between sucrose and wheel-running reinforcement was assessed in two experiments. In the first experiment, ten male Wistar rats were exposed to concurrent VI 30 s VI 30 s schedules of wheel-running and sucrose reinforcement. Sucrose concentration varied across concentrations of 2.5, 7.5, and 12.5%. As concentration increased, more behavior was allocated to sucrose and more reinforcements were obtained from that alternative. Allocation of behavior to wheel running decreased, but obtained wheel-running reinforcement did not change. Overall, the results suggested that food-deprived rats were sensitive to qualitative changes in food supply (sucrose concentration) while continuing to defend a level of physical activity (wheel running). In the second study, 15 female Long Evans rats were exposed to concurrent variable ratio schedules of sucrose and wheel-running, wheel-running and wheel-running, and sucrose and sucrose reinforcement. For each pair of reinforcers, substitutability was assessed by the effect of income-compensated price changes on consumption of the two reinforcers. Results showed that, as expected, sucrose substituted for sucrose and wheel running substituted for wheel running. Wheel running, however, did not substitute for sucrose; but sucrose partially substituted for wheel running. We address the implications of the interrelationships of sucrose and wheel running for an understanding of activity anorexia.

Key words: choice, reinforcement value, substitutability, activity anorexia, behavioral economics, sucrose, wheel running, lever press, rat

Activity anorexia occurs when rats are placed on food restriction and provided with the opportunity to run. The initial effect is that food intake is reduced, body weight declines, and wheel running increases. As running escalates, food intake drops off and body weight plummets downward, further augmenting wheel running and suppressing food intake. The result of this cycle is emaciation and, if allowed to continue, the eventual death of the animal (Epling & Pierce, 1991, 1996; Epling, Pierce, & Stefan, 1983; Routtenberg, 1968; Routtenberg & Kuznesof, 1967).

One reason this phenomenon is of considerable interest is because it defies intuition based on assumptions of energy balance. Specifically, the increased expenditure of energy (wheel

running) at a time when food intake is limited seems counterintuitive to survival and reproduction (see Pierce, 2001 for an evolutionary account). Activity anorexia in rats also shares features observed in human anorexia. Understanding the interplay between eating and physical activity may be informative in the treatment of a subset of human anorexia in which food restriction is combined with heightened levels of activity.

In the analysis of food intake and physical activity, operant investigations of the reinforcement value of wheel running and eating can play a central role. For example, Pierce, Epling, and Boer (1986) investigated the interrelationship between food and wheel-running reinforcement. These researchers demonstrated that the reinforcing value of food, as indexed by a progressive-ratio procedure, was reduced when rats ran in a wheel prior to responding for food reinforcement; also, the reinforcing value of running was increased when rats were food deprived. The interrelationship between these two reinforcement effects is central to the theory of activity anorexia proposed by Epling and Pierce (1996). More recently, Belke, Pierce, and Jensen (2004) used operant procedures to show that prefeeding rats prior to reinforce-

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ment sessions had only transient effects on wheel running and responding for the opportunity to run, when body weight remained constant. In contrast, prefeeding caused a sustained decrease in wheel running and responding for the opportunity to run when the pre-fed amount raised body weight.

The present study also uses operant procedures to analyze the interrelationship between food and wheel-running reinforcement. In the paradigm in which activity anorexia usually is studied, the opportunity to run and the opportunity to eat do not occur concurrently. Typically, animals are given the opportunity to run in a wheel for 22.5 hr without access to food and then given the opportunity to consume food without the opportunity to run in the remaining 90 min—a procedure ensuring that wheel running does not compete with eating

This separation of the opportunities to eat and run removes the element of choice from the activity anorexia procedure. An energy balance perspective would suggest that given a choice between running and eating, food-restricted animals would most likely choose to eat rather than run. That is, feeding directly increases the animal's net energy balance but running is energy costly in terms of calories used. This assumption is embodied in Collier's (1970, p. 575) statement that "since in the long run, it is better to eat than to run, running as we have shown, is a weak reinforcer". Food deprivation (and body weight decline) is expected to increase the reinforcing value of both of these reinforcers; however, because the reinforcing value of eating had greater survival and reproductive value than running, food should be preferred.

The present study sought to examine these assumptions about the relationship between running and eating using a concurrent operant procedure (see Aparicio & Baum, 1997, for an operant approach to animal foraging). When food-deprived animals are given the opportunity to choose directly between running and eating, how will they choose? Under what conditions will running be selected over food and when will food be chosen over running? This study represents a starting point for addressing these central questions. A concurrent variable-interval schedule (*conc VI VI*) of wheel running and sucrose reinforcement was used to investigate the possibility

that animals would abandon wheel running as sucrose concentration increased; rates of reinforcement were not varied so that assessment of matching and response bias (or preference) is not possible. Interval schedules were programmed because these contingencies maintain a distribution of behavior when the amount of reinforcement is different on the alternatives.

The problem of reinforcement value or efficacy of wheel running and sucrose also is raised by the present study. A recent experiment by Belke and Hancock (2003) placed rats on a single operant schedule and showed that 0.1 ml of a 2.5% sucrose solution maintained a similar rate of responding as an opportunity to run in a wheel for 15 s. At concentrations above 2.5%, responding for sucrose was greater; below 2.5% responding maintained by sucrose was less. Based on these results, Belke and Hancock (2003, p. 253) concluded that "the value of an opportunity to run for 15 s was approximately equal to the value of a drop of 2.5% sucrose solution for these rats".

Belke and Hancock's (2003) results suggest that, in the present study, rats exposed to a concurrent schedule of wheel running and sucrose would not differ in allocation of time and behavior between an opportunity to run for 15 s and the opportunity to consume a 0.1 ml of 2.5% sucrose solution. If the sucrose concentration is greater than 2.5%, then more behavior would be allocated to the sucrose alternative. With lower concentrations, more behavior would be allocated to the wheel-running alternative. Even though the duration of the opportunity to run in the present study is 30 rather than 15 s, this prediction still holds because the reinforcement value of wheel running, as indexed by preference, does not vary with duration (Belke, 2006).

Behavioral economics provides a way of describing the allocation of behavior between commodities such as sucrose and wheel running. For example, the imposed food restriction that initiates activity anorexia can be conceptualized as a substantial increase in the price of food, resulting in reduced food consumption. Low food consumption, in turn, increases consumption of physical activity—suggesting that food and physical activity may be economic substitutes. That is, an increase in the price of one commodity leads to a decline

in consumption of that commodity, but an increase in the consumption of another commodity because the latter meets, to some degree, a need fulfilled by the former (see Green & Freed, 1993, for a review of behavioral economic concepts). Consistent with this assertion, Brooks, Liu, and Pirke (1990) proposed that hyperactivity compensates for neurotransmitter changes induced by semi-starvation. Specifically, Brooks et al. (1990) showed that semistarvation decreased hypothalamic norepinephrine (NE) and dopamine (DA) whereas hyperactivity increased them. Taken together, these observations suggest the possibility of a substitutable relation between wheel running and sucrose. In Experiment 1, animals were exposed to concurrent VI VI schedules of wheel-running and sucrose reinforcement in an initial attempt to describe the distribution of behavior between these alternative commodities.

EXPERIMENT 1 METHOD

Subjects

Ten male Wistar rats, obtained from Charles River Canada, St Constant, Quebec, served as subjects. Half of the rats, those designated ID, were 5 months old and experimentally naïve at the beginning of the concurrent-operant training phase of the experiment. The remaining animals, designated KC, were approximately 1 year old at the beginning of this phase. These rats had been trained by undergraduate students to press a lever in a standard operant conditioning chamber; the KC rats also participated in an operant experiment involving wheel-running reinforcement prior to training for the current experiment.

The rats were housed individually in polycarbonate cages (480 mm long by 270 mm wide by 220 mm high) in a holding room on a 12 hr light/dark cycle, with the lights coming on at 0800. Each rat was fed sufficient food following an experimental session to maintain a target body weight of 335 ± 10 g (i.e., approximately 85% of free-feeding body weight, which was determined after each animal reached an adult body weight of approximately 400 g). This body-weight regime was mandated by the institutional animal care committee that prohibited imposition of

food restriction on animals prior to attainment of adult body weight. Distilled water was available at all times in the home cage.

Apparatus

Four activity wheels were used for the experimental sessions; two Wahmann (355 mm in diameter) and two Lafayette Instruments (350 mm in diameter) activity wheels. All wheels were located in sound-attenuating shells equipped with fans to mask extraneous noise and to provide ventilation. A solenoid-operated brake was attached to the base of each wheel. When the solenoid was operated, a rubber tip attached to a metal shaft contacted the outer rim of the wheel and brought the wheel to a stop. Twenty-four volt DC lights mounted on the wheel frame served to illuminate the interior of the wheel chamber. Revolutions were recorded by a microswitch attached to the wheel frame.

Plexiglas panels (162 mm high by 181 mm wide by 5 mm thick) that held two response levers, two stimulus lights, and a solution receptacle were attached to the wheel frame by Velcro. The levers were 151 mm wide, 45 mm apart, and extended 20 mm beyond the surface of the panel. They were located 119 mm from the base of the panel and required between 0.3 and 0.4 N of force to close the microswitch. Levers were paired according to the force requirement. A solution receptacle (38 mm by 31 mm by 61 mm) was located in the space between the two levers. Sucrose solution was contained in a cylindrical dispenser and delivered into the receptacle via a solenoid valve controlled by a Lafayette Instruments Co. Model 80201 liquid dispenser. Sucrose dispensers were 38 mm in diameter, 108 mm long, and held in place by a metal clamp above the receptacle. When the panel was attached to the wheel, the levers extended through an opening (70 mm by 90 mm) and were 75 mm above the floor of the wheel. Yellow LED lights (3 mm in diameter) were located 7 mm above each lever. Control of experimental events and recording of data were handled by a Borland Turbo Pascal 4.0 program run on IBM PC computers interfaced to the wheel through the parallel port.

Training Procedure

The training procedure was similar to that described in Belke and Belliveau (2001).

Training the animals to press for the opportunity to run in a wheel occurred in a different set of running wheels equipped with retractable levers (MED Associates ENV-112), a solenoid-operated brake, and 24-V DC lights. In this phase, the opportunity to run for 60 s was made contingent upon a single press (FR 1) of the retractable lever. A lever press caused the lever to retract and the brake to release. The wheel was free to turn for 60 s. After 60 s the brake was asserted and the retractable lever extended. A session terminated when 30 reinforcers were completed. Next the schedule of reinforcement was changed systematically in the following sequence: variable ratio (VR) 3, VR 5, and VR 9. Subjects remained on each schedule about 4 days before advancing to the next schedule.

Following this initial training phase, the animals were moved from the wheels equipped with the retractable levers to the wheels equipped with the Plexiglas panels to begin training on concurrent schedules of wheel-running reinforcement. They first were exposed to sessions in which only the right or left lever was operative. Only the stimulus light above the operative lever was illuminated, and the light was briefly extinguished for 0.08 s when a lever press occurred. The reinforcement schedule was VI 30 s and the reinforcer was the opportunity to run for 30 s. When the programmed interval elapsed and a response occurred on the operative lever, the stimulus light was extinguished and the brake was released, leaving the wheel free to turn for 30 s. The 24-V DC lights attached to the wheel frame were illuminated during the reinforcement period. After 30 s, the brake was enabled, the 24-V DC lights illuminating the wheel chamber (chamber lights) were extinguished, and the stimulus light was illuminated once more. Each animal was exposed to five sessions with one lever operative, and then five sessions with the other lever operative. Following this, the animals were exposed to a concurrent (*conc*) VI 30-s VI 30-s schedule for 20 days. A changeover delay (COD) of 0.5 s was in effect to diminish the reinforcement of switching between alternatives. This relatively brief COD was maintained as several animals were not obtaining reinforcement on both alternatives. To prevent the long pauses that typically follow the termination of a wheel-running reinforcer from affecting the opera-

tion of the concurrent VI VI schedules, VI schedules on both alternatives did not advance until the first response following the termination of a reinforcer from either alternative. Variable-interval schedules also were programmed not to advance during reinforcement periods. The rats were kept on the concurrent VI 30 VI 30 schedule of reinforcement for another 16 days to determine side biases. The data from these trials were recorded as baseline condition data and were used in an additional analysis in the results.

The rats then were exposed to sessions in which only one lever was operative and presses to this lever produced a drop of approximately 0.1 ml of 7.5% (w/v) sucrose solution as a reinforcer. If a side bias was present, the nonpreferred lever was designated the lever that yielded the sucrose solution. Only the stimulus light above the operative lever was illuminated. When sucrose was delivered, the chamber lights were briefly illuminated. Sessions took place in the running wheel and terminated after 30 min. Five rats were exposed to the left lever being operative and 5 were exposed to the right lever being operative. After 2 days on the sucrose lever, the rats were exposed to 2 days during which the other lever was operative and provided the opportunity to run for 30 s. This pattern continued for 10 days before the rats were exposed to the experimental conditions.

Experimental Procedure

For the experimental conditions, both levers were operative and both stimulus lights were illuminated. The reinforcement schedule was a modified concurrent VI 30 VI 30 schedule. Completion of the requirement on one lever provided the opportunity to run for 30 s, the other provided a drop of sucrose solution. A nominal reinforcer duration of 1 s was assumed for the sucrose reinforcer. For half the rats, the opportunity to run was associated with the left lever; for the remaining rats, the right lever. Sucrose concentrations were varied over values of 2.5, 7.5, and 12.5 percent. Table 1 shows the order of concentrations for each rat. Sessions terminated after 60 min.

Performance at a given concentration was judged to be stable when three criteria were met: a) a minimum of 20 sessions was completed, b) the difference between the highest and lowest response proportion over

Table 1

Order of sucrose concentrations for each rat and the assignment of wheel-running (W) and sucrose (S) reinforcers with the left (L) and right (R) levers.

| Rat | Assignment (L/R) | Sucrose concentration | | |
|------|------------------|-----------------------|--------|-------|
| | | First | Second | Third |
| ID1 | W/S | 2.5% | 12.5% | 7.5% |
| ID6 | S/W | 7.5% | 2.5% | 12.5% |
| ID12 | W/S | 7.5% | 2.5% | 12.5% |
| ID17 | W/S | 7.5% | 12.5% | 2.5% |
| ID19 | S/W | 12.5% | 2.5% | 7.5% |
| KC4 | S/W | 2.5% | 7.5% | 12.5% |
| KC8 | W/S | 2.5% | 7.5% | 12.5% |
| KC9 | S/W | 12.5% | 7.5% | 2.5% |
| KC15 | W/S | 12.5% | 7.5% | 2.5% |
| KC17 | S/W | 7.5% | 12.5% | 2.5% |

the last five consecutive sessions was no greater than 0.05, and c) there was no trend, either increasing or decreasing, in the last three sessions. If these criteria were not met after 40 sessions, however, the sucrose concentration was changed.

Lever presses, time spent on, changeovers to, and reinforcers obtained from each alternative were recorded during each session, as well as number of wheel revolutions. Time on an alternative was defined by changeovers; that is, an animal was considered being on an alternative, and time was accumulated, until a response was made on the other alternative. Lever presses and time spent on the alternatives were used to obtain measures of behavior allocation. Variation in behavior allocation as a function of changes in sucrose concentration was analyzed by ANOVAs with repeated measures. Paired *t*-tests were used to compare measures of behavior allocation and obtained reinforcers at the 2.5% sucrose concentration. All analyses were based on data from the last five sessions at each concentration (see Appendix A).

RESULTS

Figure 1 depicts the allocation of time between sucrose (unfilled circles) and wheel running (filled circles) as a function of sucrose concentration for each rat. In addition, time allocation to the two alternatives during the baseline condition when both alternatives provided the opportunity to run is depicted as unfilled and filled squares. The alternative represented by the unfilled square was the

alternative that later was changed to sucrose reinforcement. Time values were plotted on a logarithmic scale because decreases in time allocation to wheel running were less than increases to sucrose. On a linear scale this difference obscured changes in time allocation to the wheel-running alternative.

Time allocation was first corrected for postreinforcement pauses (PRPs) because the schedules did not operate during pauses (see Table 2). Median pauses usually were longer following wheel running and systematically decreased with concentration following wheel running, $F(2,18) = 7.96$, $p < .01$, but not sucrose. Table 2 shows systematic decreases in median pauses following wheel running for five rats; nonsystematic changes occurred in four rats. A consequence of the decline in PRPs following wheel running was an increase in time available to allocate between the alternatives. At 7.5% and 12.5% concentrations, time allocated between the alternatives increased, on average, by 297 and 400 s.

As depicted in Figure 1, time allocated to sucrose increased with concentration, $F(2,18) = 16.37$, $p < .001$. Mean time allocations for the 2.5, 7.5, and 12.5% concentrations were 582.45, 1067.2, and 1214.35 s, respectively. Systematic increases with concentration are evident for seven rats. In contrast, time spent on the wheel-running alternative decreased, $F(2,18) = 12.76$, $p < .001$, as concentration increased. Mean time allocations were 584.24, 396.47, and 351.87 s, respectively. Systematic decreases are evident for five rats. For the remaining rats, time allocated at 12.5% was less than at 2.5%; however, allocation at 7.5% did not fall between the other two values—most often it was lower than at 12.5%. Although time allocation to sucrose increased and to wheel running decreased, the magnitude of the changes differed. Typically, increases in time allocated to the sucrose alternative were greater than decreases to wheel running.

Comparisons between reinforcer types showed that at 2.5%, 3 rats allocated more time to the sucrose alternative whereas 5 allocated more time to wheel running. At 7.5%, 7 rats allocated more time to sucrose. At 12.5%, 8 rats allocated more time to the sucrose alternative. Paired *t*-test comparisons showed that time allocation to the sucrose alternative was significantly higher at 7.5% and

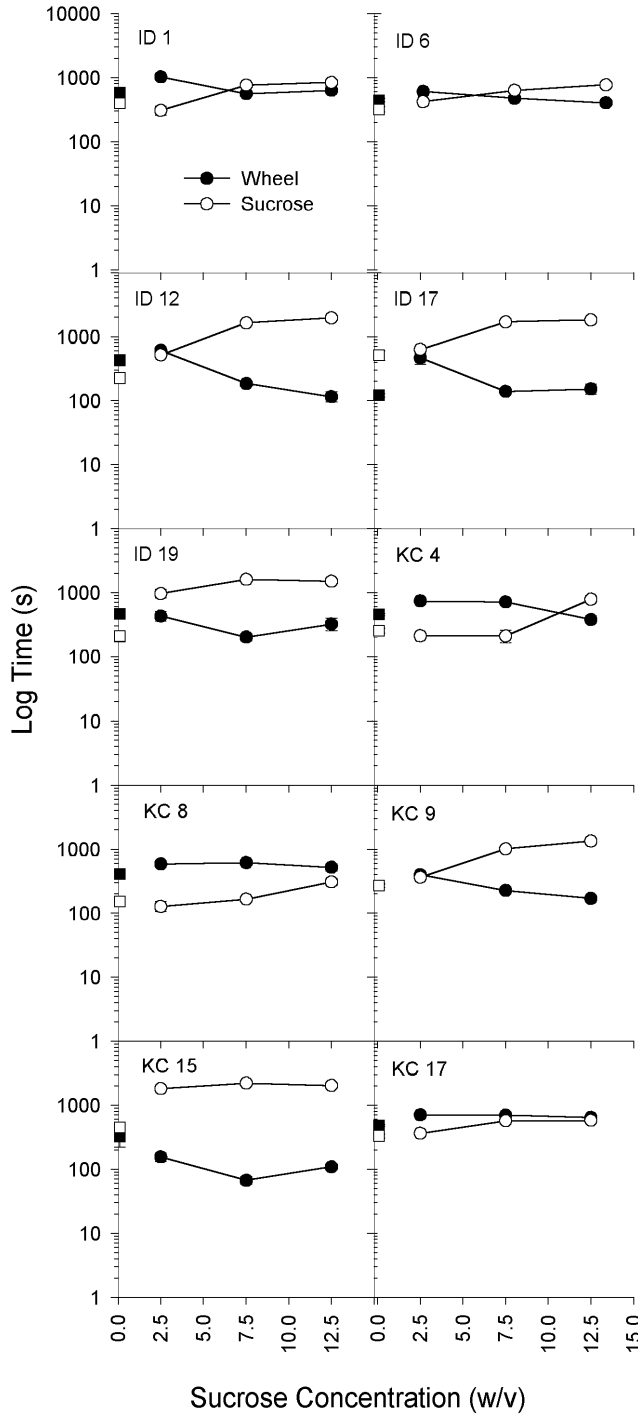


Fig. 1. Mean time (in s) allocated to the wheel running (filled circles) and sucrose (unfilled circles) alternatives plotted on a logarithmic scale as a function of sucrose concentration for each rat. Mean time allocations during the baseline condition in which both alternatives produced the opportunity to run are plotted as filled and unfilled squares along the ordinate axis. The unfilled square represents the alternative that was changed to produce sucrose reinforcement. Standard error values are plotted for each mean. (Note: some standard errors are too small to be seen.)

Table 2

Median postreinforcement pause durations (in s) following wheel-running and sucrose reinforcers in the 2.5, 7.5, and 12.5% concentration conditions for each rat.

| Rat | Wheel running | | | Sucrose | | |
|-------|---------------|------|-------|---------|------|-------|
| | 2.5% | 7.5% | 12.5% | 2.5% | 7.5% | 12.5% |
| ID 1 | 18.7 | 27.5 | 13.4 | 5.2 | 3.7 | 6.3 |
| ID 6 | 27.6 | 22.9 | 16.4 | 7.9 | 7.7 | 9.6 |
| ID12 | 34.7 | 9.5 | 5.9 | 6.1 | 7.9 | 6.3 |
| ID 17 | 46.7 | 16.8 | 16.6 | 13.3 | 10.5 | 8.7 |
| ID 19 | 38.8 | 12.4 | 6.2 | 7.7 | 12.5 | 9.7 |
| KC 4 | 36.5 | 52.9 | 28.6 | 4.5 | 4.1 | 10.0 |
| KC 8 | 84.0 | 69.5 | 72.3 | 4.1 | 3.1 | 5.0 |
| KC 9 | 50.5 | 30.2 | 22.9 | 5.6 | 7.1 | 6.3 |
| KC 15 | 10.5 | 5.1 | 7.8 | 8.9 | 5.9 | 7.0 |
| KC 17 | 27.9 | 22.6 | 29.1 | 3.5 | 5.2 | 4.4 |
| Mean | 37.6 | 26.9 | 21.9 | 6.7 | 6.8 | 7.3 |

12.5%, $t(9) = -3.36, p < .01$; $t(9) = -2.25, p < .05$ (both one tailed).

Finally, time allocations under baseline conditions show that 7 rats allocated less time to the alternative that was changed to sucrose. Consequently, an initial side bias did not play a role in the increase in time allocation to this alternative as concentration increased.

Figure 2 shows the equivalent data for response allocation. As was the case with time, responses allocated to the sucrose alternative increased with concentration, $F(2,18) = 4.77, p < .05$. Eight rats display systematic increases in responses allocated to the sucrose alternative. The remaining 2 show higher responses at 12.5% than at 2.5%; however, responses at 7.5% were lower and higher than at 12.5%, respectively. With respect to the wheel-running alternative, responses allocated to this alternative decreased as concentration increased, $F(2,18) = 4.25, p < .05$. Systematic decreases are evident for 4 rats. The remaining rats did not show monotonic decreases with higher values of sucrose concentration. As with time allocation, increases in responses to the sucrose alternative were greater than decreases to wheel running.

Comparisons across reinforcer types show that at 2.5% 4 rats allocated similar numbers of responses to both alternatives. At 7.5%, more responses were allocated to the sucrose alternative by 5 rats. For the 12.5% concentration, 8 rats allocated more responses to sucrose. Paired t -test comparisons showed that responses allocated to the sucrose alternative were greater when the concentration was 12.5%, $t(9) = -2.01, p < .05$ (one tailed.)

Baseline allocations showed that with the exception of 1 rat, fewer responses were allocated to the alternative that would be changed to sucrose. Consequently, as with time allocation, the increases in response allocation with concentration were not influenced by side bias.

Changes in behavior allocation can yield changes in obtained reinforcement. Figure 3 depicts for each rat the number of reinforcers obtained from the two alternatives as a function of concentration, as well as allocations under the baseline condition. Usually, the number of sucrose reinforcers increased with concentration, $F(2,18) = 13.16, p < .001$. On average, 25.3, 38.6, and 44.5 sucrose reinforcers were obtained when concentrations were 2.5, 7.5, and 12.5%, respectively. Eight rats showed systematic increases in obtained sucrose reinforcers with increases in concentration. For the remaining 2 rats, obtained sucrose reinforcers were not monotonically related to sucrose concentration. In contrast, the number of obtained wheel-running reinforcers did not vary systematically with concentration, $F(2,18) = 0.15$. On average, 25.8, 25.2, and 25.4 wheel-running reinforcers were obtained across the 2.5, 7.5, and 12.5% concentrations, respectively. Across individual animals, no consistent pattern of changes is evident.

Comparisons between the alternatives show that two, six, and nine rats obtained more sucrose reinforcers at 2.5%, 7.5% and 12.5% concentrations, respectively. Paired t -test comparisons showed that more reinforcers were obtained from the sucrose alternative when

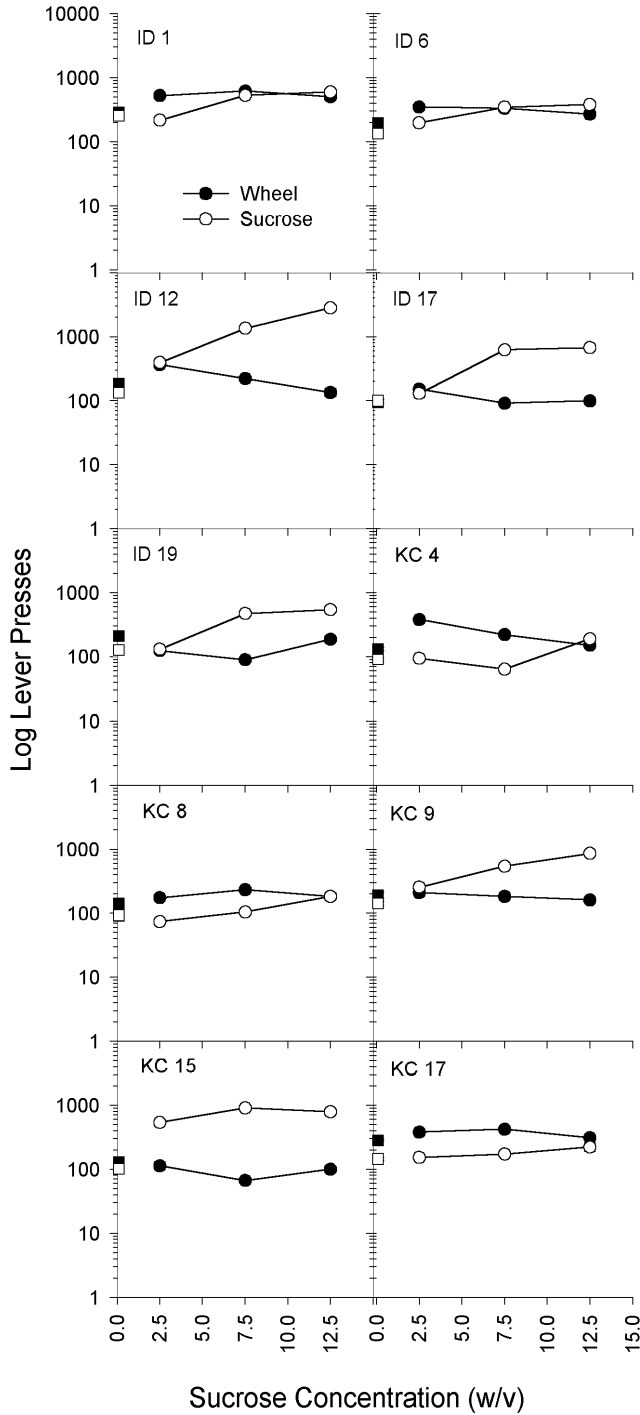


Fig. 2. Mean number of responses (lever presses) allocated to the wheel running (filled circles) and sucrose (unfilled circles) alternatives plotted on a logarithmic scale as a function of sucrose concentration for each rat. Mean response allocations during the baseline condition in which both alternatives produced the opportunity to run are plotted as filled and unfilled squares along the ordinate axis. The unfilled square represents the alternative that was changed to produce sucrose reinforcement. Standard error values are plotted for each mean. (Note: some standard errors are too small to be seen.)

the concentrations were 7.5 and 12.5%, $t(9) = -1.86$, $p < .05$; $t(9) = -2.87$, $p < .01$ (both one tailed).

The data from the baseline condition show no systematic differences in obtained reinforcers between the two alternatives when both provided the opportunity to run. Figure 3 also shows that when the rats were moved from the concurrent schedule of wheel running (baseline) to sucrose and wheel running, the number of obtained wheel-running reinforcers on the unchanged alternative increased markedly for every rat. As a result of this increase, the average numbers of obtained wheel-running reinforcers in the 2.5%, 7.5% and 12.5% conditions were 84%, 82%, and 82% of the average numbers obtained in the baseline condition ($M = 30.9$). This tendency to defend a level of wheel running may have contributed to the lack of a decline in wheel-running reinforcers as sucrose concentration increased.

DISCUSSION

The distribution of behavior between wheel running and sucrose varied systematically with sucrose concentration. As concentration increased, more behavior was allocated to sucrose, less to wheel running. Increases for sucrose, however, were not accompanied by equivalent decreases for wheel running. Similarly, sucrose reinforcers increased while obtained wheel-running reinforcers remained unchanged. Thus, the rats were able to reallocate behavior to obtain the sweeter, more nutritive food (sucrose) and maintain their levels of wheel running; they likely did this by decreasing postreinforcement pauses on the wheel-running alternative.

This decline in the pause following wheel running, with increased efficacy of an alternative source of reinforcement in the context, is the first demonstration of such an effect. Postreinforcement pauses are of interest with this particular reinforcer because they can convey the effects of variables that affect the efficacy of wheel running as a reinforcer. Previous research showed that postreinforcement pauses following wheel running were most strongly determined by body weight (Belke, 1996, 2004) and duration of the running period (Belke 1997; Belke & Dunbar, 1998) but weakly affected, if at all, by the schedule of reinforcement (Belke, 1996; Belke

& Dunbar, 1998). The current result shows that pause duration can be modified by motivation to engage in other behaviors in the context.

Also of note is the pattern of increased allocation to and reinforcers obtained from the sucrose alternative without an equivalent decline in obtained wheel-running reinforcers. One interpretation for this pattern is that food-deprived animals are sensitive to the quality of food in their environment, but are motivated also to maintain food-related travel (Pierce, 2001). In other words, food-deprived animals continue to respond for physical activity rather than show exclusive preference for a high-calorie alternative.

From a behavioral economic perspective, our results suggest that food (sucrose) and physical activity (wheel running) are not highly substitutable. If these commodities were substitutes, a reduction in the price of sucrose (i.e., increase in concentration) would lead to a marked increase in the consumption of sucrose and a marked decrease in the consumption of wheel running. Although animals moderately increased consumption of sucrose, consumption of wheel running did not change. Wheel running may be marginally substitutable with, or be independent of, sucrose.

This qualitative analysis of the economic relationship between sucrose and wheel running must be regarded with caution for two reasons. Interval schedules, unlike ratio schedules, are relatively insensitive to changes in response rate. Consequently, rats could not easily compensate for increased concentration by reducing the rate of occurrence of wheel-running reinforcers. Also, income was not adjusted as concentration varied. To obtain only the effect of price on consumption, income must be adjusted to allow the same level of consumption at each price. Experiment 2 was designed to rectify these problems and provide a precise quantitative assessment of the substitutability between sucrose and wheel running.

EXPERIMENT 2

Green and Rachlin's (1991) procedure for assessing the substitutability of qualitatively different reinforcers was used to assess the relationship between wheel running and su-

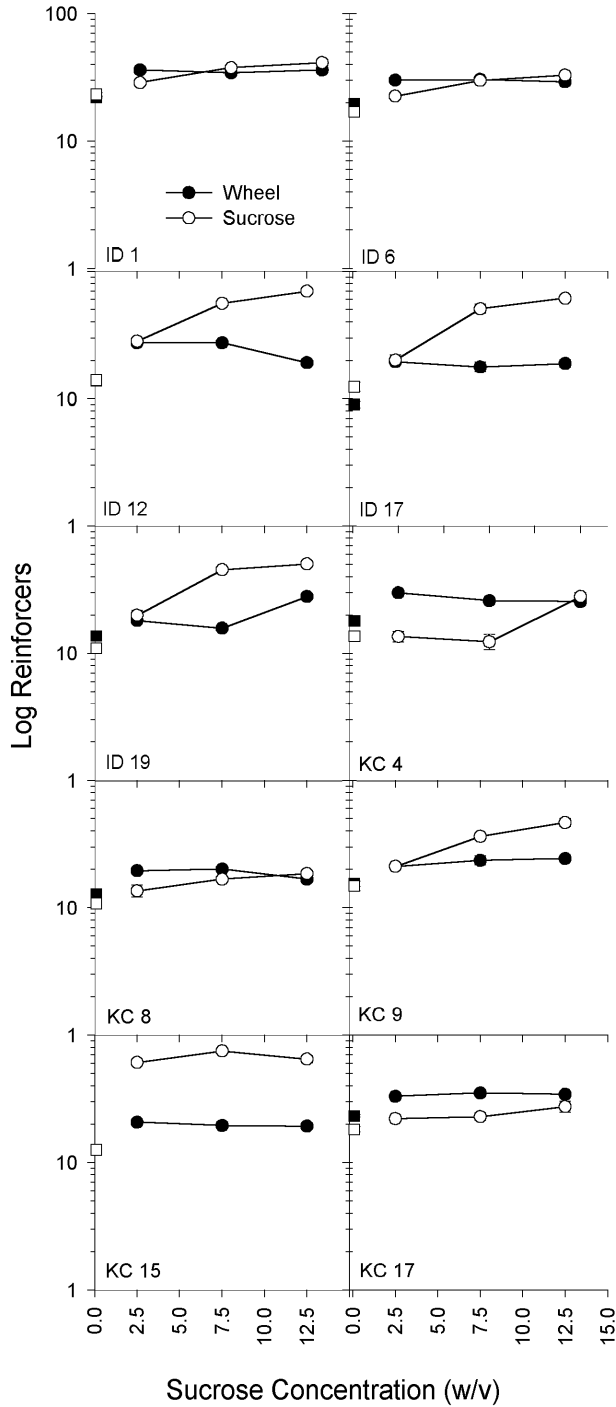


Fig. 3. Mean number of reinforcers obtained from the wheel running (filled circles) and sucrose (unfilled circles) alternatives plotted on a logarithmic scale as a function of sucrose concentration for each rat. Mean obtained reinforcers during the baseline condition in which both alternatives produced the opportunity to run are plotted as filled and unfilled squares along the ordinate axis. The unfilled square represents the alternative that was changed to produce sucrose reinforcement. Standard error values are plotted for each mean. (Note: some standard errors are too small to be seen.)

crose. In this procedure, animals are given an income of a total number of responses to allocate between two alternative sources of reinforcement; the session terminates when these responses have been spent. The prices of both reinforcers as determined by concurrent VR schedules are varied, with income adjusted, to assess the effect of income-compensated price changes on consumption of both reinforcers.

The potential effects of price changes on the pattern of consumption representing different economic relationships between commodities are graphically portrayed in Figure 4. In this figure, the lines represent budget lines and the symbols represent different combinations of quantities of reinforcers X and Y. The budget lines represent all possible combinations of X and Y reinforcers that can be purchased given the prices of these commodities and the total income available to spend. Within these constraints, combinations can vary between all X and no Y to all Y and no X reinforcers.

The economic relationship is determined by the extent to which consumption of the two commodities under unequal prices shifts away from the consumption level when prices are equal (triangle). The dashed line represents all possible combinations where the price of commodity Y is halved and the price of commodity X is doubled; the stippled line represents the reverse.

When consumption does not commensurate with price changes (circles), commodities are considered complements. In Figure 4, consumption of the lower-priced commodity does not double when its price is halved, and consumption of the higher-priced commodity is not reduced by a half when its price is doubled. Thus, changes in consumption are proportionally less than the price changes. For example, if the two commodities typically are purchased and consumed together, such as spaghetti and spaghetti sauce, then the increase in consumption of spaghetti with a price decrease is likely to be less than expected if the price of spaghetti sauce concurrently increases. In contrast, when consumption varies in accord with respective price changes (squares), commodities are considered independent. Consumption of the lower-priced commodity doubles when the price is halved while consumption of the higher-priced commodity halves when the price is doubled. In

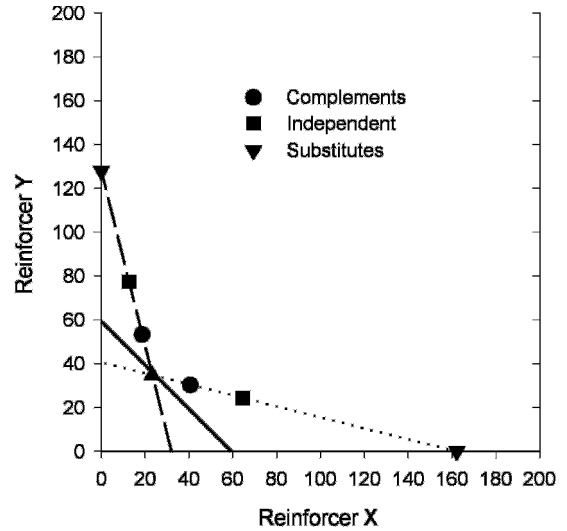


Fig. 4. Changes in consumption of Reinforcers X and Y with changes in price define the commodities as complements, independents, or substitutes (see text for explanation).

each case, consumption of each commodity changes with price, but has no effect on consumption of the other commodity. For example, consumption of shoes will change with changes in the price of shoes and likewise for consumption of soda pop; however, changes in the consumption of soda pop are unlikely to be affected by changes in the price of shoes. Finally, when consumption shifts even farther along the budget lines representing the changed prices (inverted triangles), commodities are considered substitutes. Consumption of the lower-priced commodity more than doubles when its price is halved; moreover, consumption of the higher-priced commodity is reduced more than a half when its price is doubled. The more the changes in consumption exceed the price changes, the more substitutable the two commodities. At the extreme, if both commodities meet identical needs, they are perfect substitutes. For example, an increase in the price of coffee will lead to a greater than expected decline in consumption of coffee as consumers switch to tea which substitutes for coffee as a source of caffeine.

A quantitative estimate of substitutability (i.e., the extent of shifts in consumption with changes in price) can be calculated using the

following equation from Green and Rachlin (1991):

$$x/y = k(q/p)^m. \quad (1)$$

In Equation 1, x and y represent the responses allocated to the alternatives yielding reinforcers X and Y ; p and q are the variable-ratio requirements associated with reinforcers X and Y , respectively. The estimated parameters, k and m , are interpreted similarly to the parameters of the generalized matching equation (Baum, 1974) and represent systematic response bias and sensitivity of response allocation to changes in relative price (q/p), respectively.

Based on Equation 1, substitutability values are obtained by a linear regression of the natural log of relative response allocation, $\ln(x/y)$, on the natural log of the inverse of relative price, $\ln(q/p)$. The slope of this regression is the estimate of the sensitivity parameter, m , in Equation 1. The estimate of substitutability, s , is calculated as $m/(m+1)$. The complete derivation of Equation 1 is given by Green and Rachlin (1991, pp. 140–141) and is based on maximization of the utility from different combinations of two commodities (reinforcers).

The interpretation of substitutability (s) depends on its value. A negative value, $s < 0$, indicates that the two reinforcers are complements. A value of $s = 0$ indicates that the commodities are independent. A positive value, $s > 0$, indicates substitutability. Degree of substitutability between two commodities is captured by the value of s within the range of $0 < s < 1$. As s approaches 1, commodities approach complete substitutability. For example, sucrose completely substitutes for sucrose as wheel running does for wheel running, but sucrose may only be a partial or incomplete substitute for wheel running. In Experiment 2, rats were exposed to concurrent VR schedules of sucrose and wheel-running reinforcement, wheel-running and wheel-running reinforcement, and sucrose and sucrose reinforcement to assess the substitutability between these qualitatively similar and different reinforcers.

METHOD

Subjects

Fifteen female Long-Evans rats obtained from Charles River Breeding Laboratories, St.

Constant, Quebec, served as subjects. Prior to participating in the present study, the rats had been shaped to press a lever in a standard operant conditioning chamber by students in a conditioning course. The rats were maintained at a target weight that was approximately 85% of a free-feeding body weight taken when the weights of the rats rose just beyond 300 grams (i.e., adult weight). Target weights varied around 260 g \pm 10 g. All other conditions were as specified in Experiment 1.

Apparatus

The apparatus from Experiment 1 was used in Experiment 2.

Procedure

Training the rats to respond on a lever for the opportunity to run and on concurrent schedules of wheel-running reinforcement followed a regimen similar to that outlined in Experiment 1. Following the training phase, all rats were placed on concurrent VR 10 VR 10 schedules of wheel-running (30 s) and sucrose (0.1 ml of 7.5% w/v) reinforcement. For half the rats, sucrose was on the right; for the other half, sucrose was on the left. PRPs following wheel-running reinforcers were measured, and a 2.5-s pause was programmed to follow sucrose delivery, allowing for consumption. The budget for this initial condition was 600 lever presses.

When performance on the initial condition was judged stable, two additional conditions were arranged in which the schedule values were VR 20 VR 5 and VR 5 VR 20. The order of presentation of these additional conditions was counterbalanced across rats. A budget for each rat for each additional condition was calculated. To obtain the budget for a condition, the number of reinforcers obtained on each alternative in the initial condition was multiplied by the VR value for that alternative in the new condition. The sum of these products was the budget for the new condition. For example, if a rat obtained 10 reinforcers on the left VR 10 schedule in the initial condition and the schedule value for this alternative in the new condition was VR 20, then the 10 obtained reinforcers were multiplied by 20 to obtain a value of 200. On the right alternative in the initial condition, the rat would have obtained 50 reinforcers on

Table 3

Mean responses, time (in s), reinforcers, changeovers, and wheel revolutions on the left (L) and right (R) alternatives from the 9 sessions that met the stability criteria for each concurrent ratio schedule for the sucrose-wheel, wheel-wheel, and sucrose-sucrose reinforcer combinations for the group of rats that completed all conditions. Time spent lever pressing is exclusive of reinforcer and postreinforcement pause durations. Average session time in minutes (ST) also is provided.

| L | R | Schedule | | Responses | | Time | | Reinforcers | | CO | | Revolutions | | ST |
|---|---|----------|----|-----------|-----|------|-----|-------------|----|-----|-----|-------------|------|-----|
| | | L | R | L | R | L | R | L | R | L | R | L | R | |
| S | W | 10 | 10 | 300 | 300 | 438 | 505 | 29 | 29 | 87 | 87 | 0 | 598 | 41 |
| S | W | 20 | 5 | 369 | 362 | 653 | 868 | 18 | 72 | 101 | 102 | 0 | 1252 | 83 |
| S | W | 5 | 20 | 479 | 253 | 463 | 415 | 96 | 12 | 72 | 72 | 0 | 297 | 32 |
| W | W | 10 | 10 | 166 | 234 | 407 | 452 | 16 | 23 | 57 | 57 | 300 | 415 | 46 |
| W | W | 20 | 5 | 122 | 316 | 401 | 962 | 6 | 63 | 69 | 69 | 90 | 1027 | 82 |
| W | W | 5 | 20 | 401 | 143 | 1205 | 549 | 80 | 6 | 79 | 79 | 1296 | 102 | 107 |
| S | S | 10 | 10 | 228 | 172 | 186 | 193 | 22 | 17 | 32 | 32 | 0 | 0 | 10 |
| S | S | 20 | 5 | 110 | 414 | 106 | 279 | 5 | 82 | 32 | 32 | 0 | 0 | 13 |
| S | S | 5 | 20 | 344 | 99 | 233 | 95 | 69 | 5 | 29 | 29 | 0 | 0 | 11 |

the VR 10 schedule and the new schedule for this alternative was VR 5, then 50 reinforcers multiplied by the 5 would produce a value of 250. Consequently, the budget for the new condition for this rat would be 200 plus 250 for a total of 450 lever presses.

Budget values calculated in this manner ensured that the budget lines for the additional conditions crossed the budget line from the initial condition, at the point representing the subjects' initial allocation of obtained reinforcers from the two alternatives. A budget line was defined as the line representing all possible combinations of obtained reinforcers from the two alternatives, given the constraints of the budget and the schedule values on the two alternatives. This line would be located in a space defined by reinforcers obtained on the right alternative along the abscissa and reinforcers obtained on the left on the ordinate. For the initial condition, the budget line would run from an endpoint value on the abscissa representing all reinforcers obtained on the right alternative (i.e., $600/10 = 60$) and none on the left ($0/10 = 0$) to an endpoint on the ordinate representing no reinforcers obtained on the right alternative ($0/10 = 0$) and all reinforcers obtained on the left ($600/10 = 60$).

Following completion of the conditions with concurrent schedules of wheel running and sucrose reinforcement, the same three conditions (initial plus two additional) were repeated with wheel-running reinforcement on both alternatives. Finally, the conditions were

repeated again with sucrose on both alternatives. All aspects of the procedure were the same with the exception that the budget in the initial condition was 400 rather than 600 lever presses. This change occurred to ensure that sessions with wheel running on both alternatives would not be prohibitively longer than sessions with wheel running and sucrose.

Each condition remained in effect until a number of stability criteria were met. First, a minimum of 20 sessions had to occur before performance could be judged stable. After 20 sessions, response proportions from the last nine sessions were divided into three groups of three sessions and the average for each group was calculated. The difference between the highest and the lowest average response proportions had to be equal to or less than 0.05 and there could be no trend across the three averages. When these three criteria were met, performance was judged to be stable.

Dependent measures were the same as in Experiment 1.

RESULTS

Table 3 shows the results averaged over the nine sessions that met the stability criteria; the results are shown for each condition of each combination of reinforcers for the group. Data for individual animals are shown in Appendix B. Rats BZ 1, BZ 3, and BZ 8 failed to complete all conditions across the three reinforcer combinations due to health reasons; consequently, data from these rats were not included in subsequent analyses.

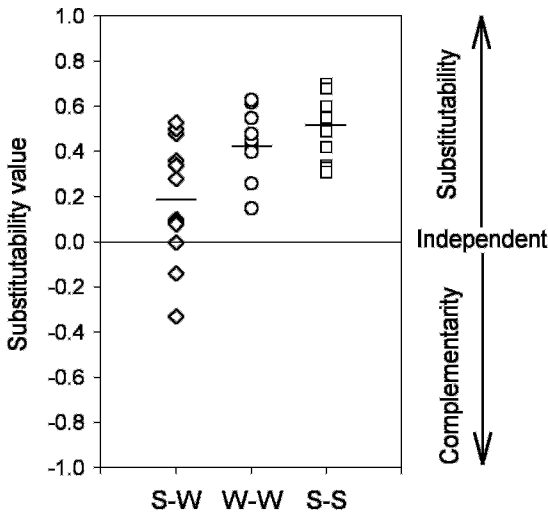


Fig. 5. Substitutability values for the wheel–sucrose, wheel–wheel, and sucrose–sucrose reinforcer combinations for each rat. Mean values are indicated by a horizontal line. Values less than 0 indicate that commodities are complements. A value of 0 indicates that the commodities are independent. Values above 0 indicate that commodities are substitutes. Degree of substitutability increases as the value increases between 0 and 1.0.

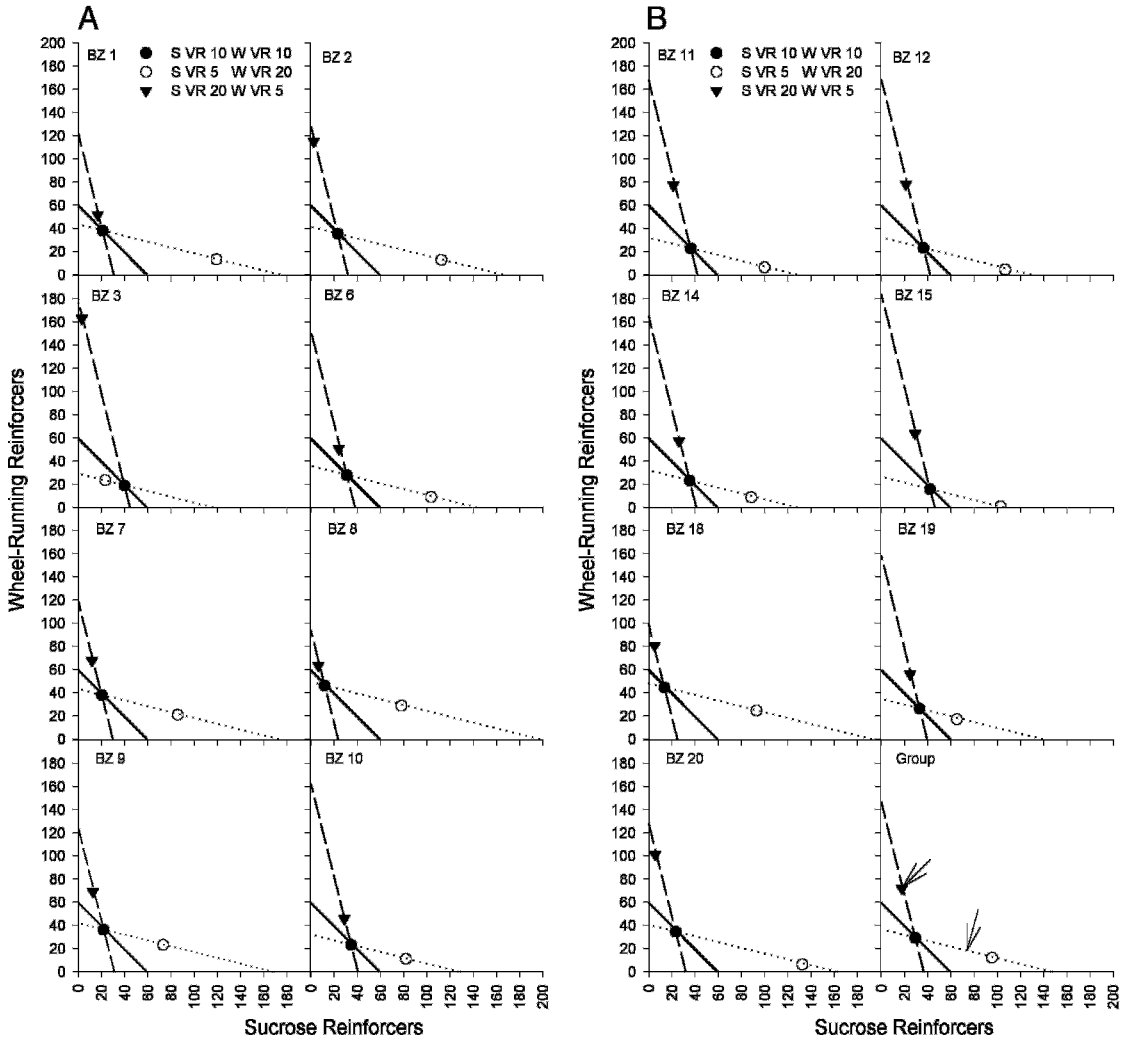
Figure 5 shows the distributions of substitutability values (s) for the sucrose–wheel, wheel–wheel, and sucrose–sucrose reinforcer combinations. Mean substitutability values for these combinations were 0.19, 0.42, and 0.51, respectively. For the sucrose–wheel combination, a paired t -test against the value of 0, representing independent commodities, showed that substitutability values were significantly greater than 0, $t(11) = 2.46$, $p = 0.03$.

Wheel–wheel and sucrose–wheel substitutability values also were compared with a paired t -test. Theoretically, a commodity should be a perfect substitute for itself. Consequently, one would predict that wheel–wheel substitutability values should be greater than sucrose–wheel values. As predicted, wheel running was more substitutable with itself than it was with sucrose, $t(11) = 2.83$, $p = .008$ (one-tailed). Similarly, a comparison between sucrose–sucrose and sucrose–wheel values revealed that sucrose was more substitutable with itself, as expected, than with wheel running, $t(11) = 4.96$, $p = .0002$ (one-tailed). Unexpectedly, however, a comparison of the substitutability values for sucrose–sucrose and wheel–wheel revealed that sucrose was a better substitute for itself than was wheel running for wheel

running, $t(11) = 3.36$, $p = .006$. Theoretically, this should not have occurred; the finding suggests that there is some difference between wheel running and sucrose (as reinforcers) that interacts with the experimental procedure to yield lower substitutability values for wheel running.

Figures 6a and 6b depict the amount of each type of reinforcer obtained on concurrent variable ratio schedules of wheel-running and sucrose reinforcement under the three different price/budget conditions for each rat and the group. Figures 7a and 7b depict the equivalent graphs for the conditions with concurrent ratio schedules of wheel-running reinforcement. Figures 8a and 8b show the same graphs for the conditions with concurrent schedules of sucrose reinforcement. This series of plots reflects the substitutability values plotted in Figure 5. Data points on the budget lines for the unequal ratios are displaced further away from the distribution in the equal ratio condition (represented by the solid circles) and closer to the ordinate and abscissa axes in the wheel–wheel and sucrose–sucrose plots. In addition, these plots also show the symmetry of the effect of the price manipulations on changes in the distribution of obtained reinforcers. Effects need not be symmetrical (see Green & Freed, 1993). Commodity A may serve as a substitute for Commodity B; however, Commodity B may not serve as a substitute for Commodity A. Although the effects appear symmetrical for wheel–wheel and sucrose–sucrose combinations, as would be expected, this was not the case for the sucrose–wheel combination. When the price of wheel running was halved and the price of sucrose was doubled, consumption shifted less than when the price of sucrose was halved and the price of wheel running doubled. This finding suggests that sucrose may partially substitute for wheel running, but wheel running does not substitute for sucrose.

Substitutability values for both the sucrose–sucrose and wheel–wheel arrangements fell substantially below the value of 1.0 that would be expected for completely substitutable commodities. Notice that a value of 1.0 requires that animals show exclusive preference for the alternative with the lower ratio requirement (lower price). Even a few responses to the alternative with the larger ratio rapidly reduce

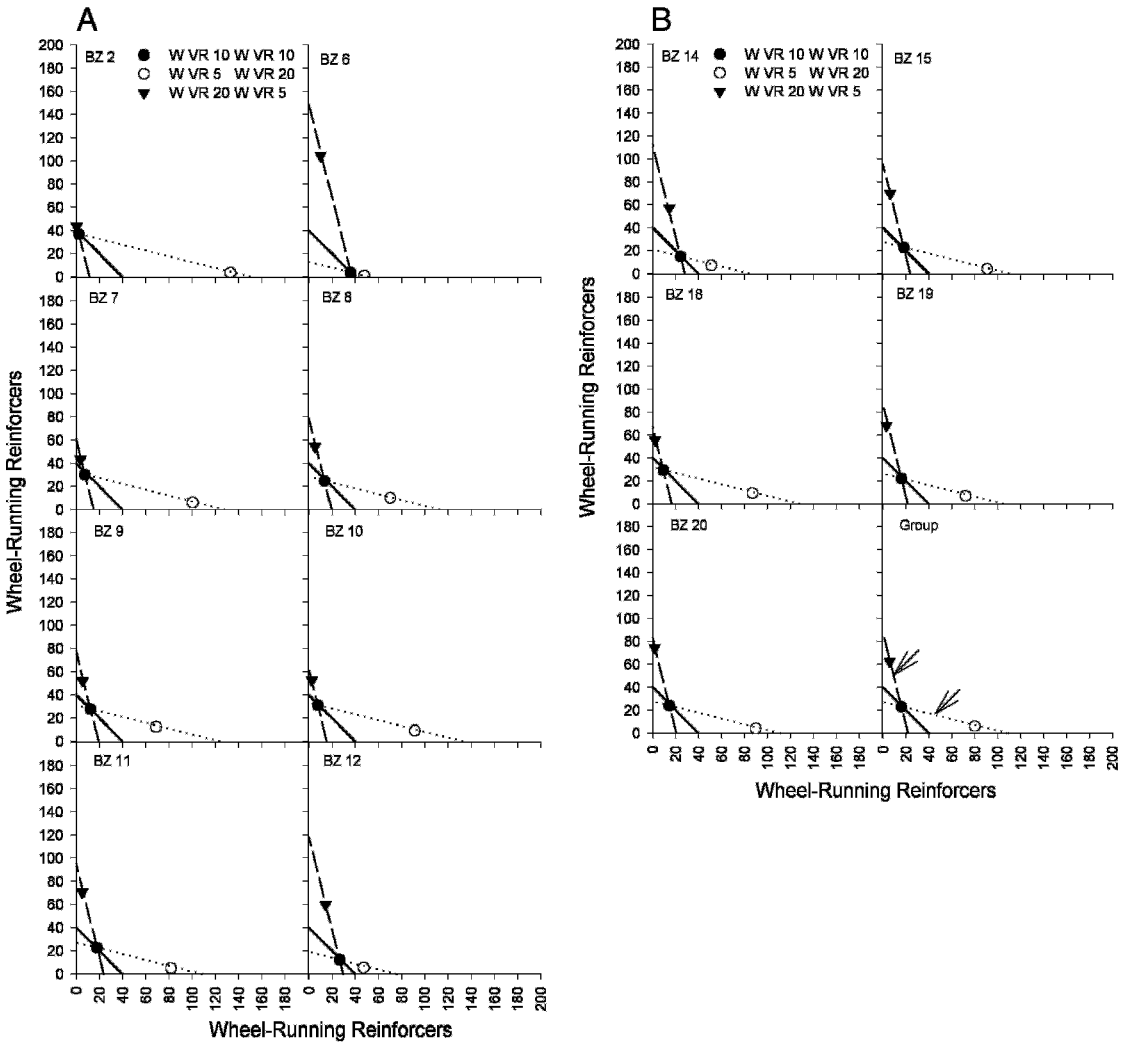


Figs. 6a and 6b. Mean number of wheel-running and sucrose reinforcers consumed under the three different price/budget conditions for the sucrose–wheel-running reinforcer combination for each rat and the group. The group graph displays the data from the 12 rats that completed all three conditions across all three combinations of reinforcer types. Arrows indicate consumption amounts that would have yielded the determination that the commodities were independent; these values were derived by generating distributions that would have produced a substitutability value of zero.

the substitutability value from the expected 1.0 value. Consequently, observed substitutability values for a commodity with itself are likely to fall below 1.0. For example, Green and Rachlin (1991) obtained substitutability values of .72 and .73 for two rats when both alternatives programmed ratio schedules of electrical brain stimulation—attributing these substitution values to “a tendency to alternate, which ensures that, however advantageous one alter-

native may be, other alternatives are occasionally sampled” (p. 141).

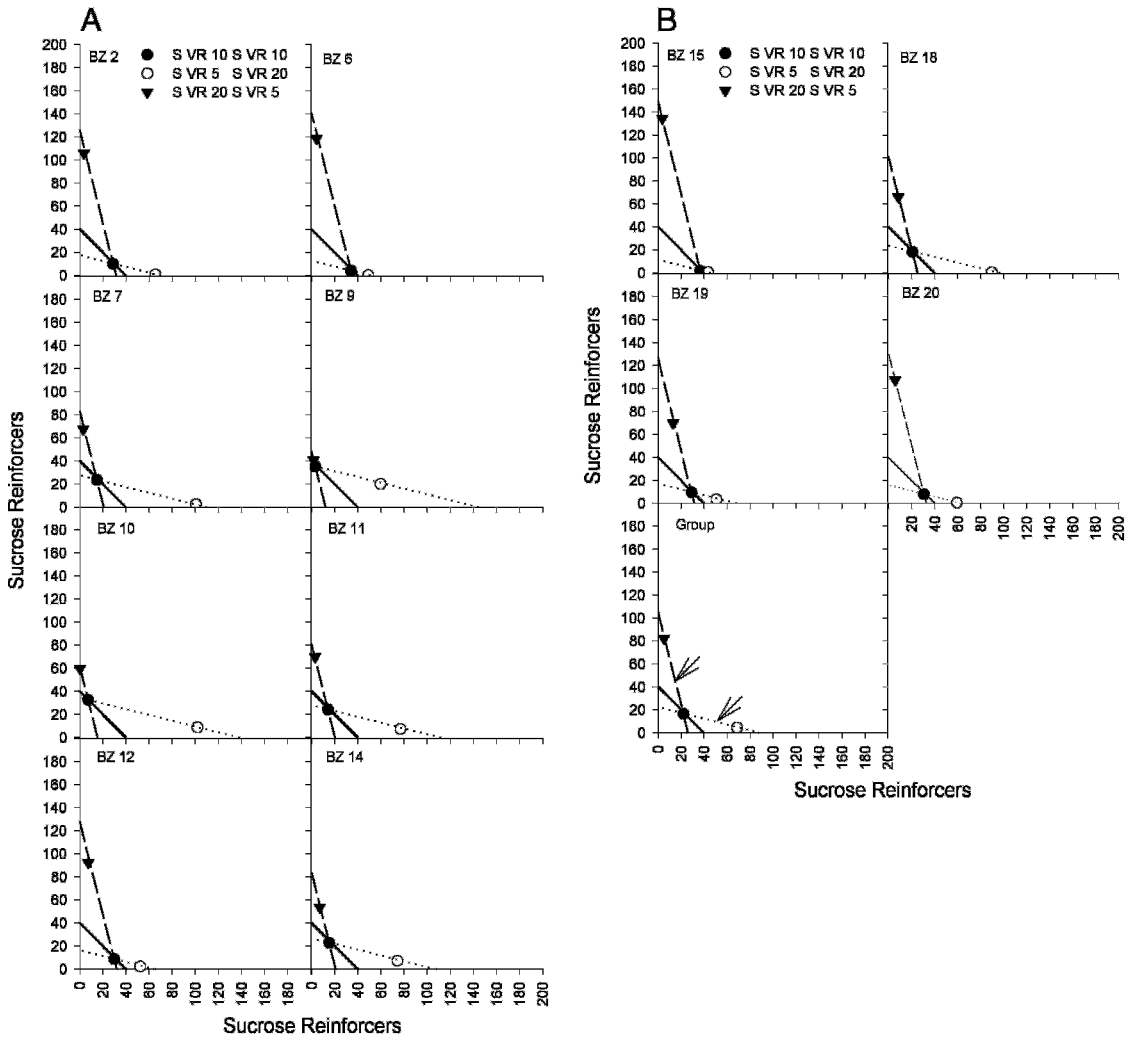
Changes between alternatives also reflect the degree of sensitivity to the contingencies of reinforcement. That is, a high level of switching is associated with low sensitivity to the ratio contingencies and, presumably, lower observed substitutability values. The relationship between switching and substitutability values is evident from correlations between the per-



Figs. 7a and 7b. Mean number of wheel-running reinforcers consumed under the three different price/budget conditions for the wheel-running-wheel-running reinforcer combination for each rat and the group. The group graph displays the data from the 12 rats that completed all three conditions across all three combinations of reinforcer types. Arrows indicate consumption amounts that would have yielded the determination that the commodities were independent; these values were derived by generating distributions that would have produced a substitutability value of zero.

centages of responses that were changeovers on the *conc* VR 10 VR 10 schedule and obtained substitutability values. For the wheel-wheel and sucrose-sucrose combinations, the correlations were $-.75$ ($p = .005$) and $-.68$ ($p = .015$), respectively. However, substitutability values obtained for the sucrose-wheel arrangement were not significantly correlated with switching on the *conc* VR 10 VR 10 schedule, $r(12) = 0.16$.

Table 4 shows the percentage of the total responses that were changeover responses calculated for each set of concurrent ratio requirements for the sucrose-wheel, wheel-wheel, and sucrose-sucrose combinations for each rat. For the sucrose-sucrose arrangement, the mean percentages of total responses that were changeovers for the *conc* VR 10 VR 10, *conc* VR 5 VR 20, and *conc* VR 20 VR 5 conditions were 16.0, 12.0, and 12.4, respec-



Figs. 8a and 8b. Mean number of sucrose reinforcers consumed under the three different price/budget conditions for the sucrose-sucrose reinforcer combination for each rat and the group. The group graph displays the data from the 12 rats that completed all three conditions across all three combinations of reinforcer types. Arrows indicate consumption amounts that would have yielded the determination that the commodities were independent; these values were derived by generating distributions that would have produced a substitutability value of zero.

tively. For the wheel-wheel combination, the equivalent percentages were 28.7, 29.2, and 29.4, respectively. The percentage of changeovers in the *conc* VR 10 VR 10 wheel-wheel condition was almost twice the percentage for the same schedule when sucrose was the reinforcer on both alternatives, $t(11) = 4.13$, $p < .002$. The higher level of changing over may account for the lower substitutability values for the wheel-wheel combination relative to those for the sucrose-sucrose combination. For the sucrose-wheel combination, the

mean percentages were 29.0, 19.3, and 27.2, respectively. The level of switching for the *conc* VR 10 VR 10 condition was the same as that when both reinforcers were wheel running. In addition, switching diminished when the response requirement for sucrose was reduced, $t(11) = 3.26$, $p = .008$, but did not diminish when the requirement for wheel running was reduced.

The data from the sucrose-sucrose combination across rats are presented in Appendix B and suggest that side biases may have played

Table 4

Percentage of total responses that were changeover responses for the concurrent VR 10 VR 10, VR 5 VR 20, and VR 20 VR 5 conditions for the sucrose-wheel, wheel-wheel, and sucrose-sucrose arrangements for each rat.

| Rat | Sucrose-wheel | | | Wheel-wheel | | | Sucrose-sucrose | | |
|-------|---------------|------|------|-------------|------|------|-----------------|------|------|
| | 10 10 | 5 20 | 20 5 | 10 10 | 5 20 | 20 5 | 10 10 | 5 20 | 20 5 |
| BZ 2 | 19.0 | 10.9 | 10.3 | 5.9 | 13.4 | 5.9 | 6.8 | 3.1 | 6.8 |
| BZ 6 | 38.2 | 23.7 | 29.8 | 13.9 | 7.6 | 30.7 | 11.0 | 2.2 | 9.7 |
| BZ 7 | 30.1 | 19.2 | 22.7 | 23.9 | 27.1 | 26.9 | 18.0 | 6.3 | 12.6 |
| BZ 9 | 38.2 | 34.3 | 44.6 | 38.1 | 45.1 | 44.7 | 13.1 | 21.8 | 16.2 |
| BZ 10 | 15.7 | 12.7 | 16.9 | 23.6 | 24.0 | 22.3 | 9.9 | 6.6 | 2.6 |
| BZ 11 | 17.3 | 15.3 | 16.2 | 30.9 | 31.4 | 24.9 | 23.7 | 25.7 | 10.4 |
| BZ 12 | 40.4 | 23.5 | 53.8 | 44.1 | 52.1 | 51.5 | 30.3 | 21.9 | 13.4 |
| BZ 14 | 38.1 | 34.6 | 38.8 | 40.4 | 43.2 | 46.2 | 31.9 | 24.0 | 29.3 |
| BZ 15 | 32.9 | 3.3 | 31.1 | 43.3 | 24.4 | 37.7 | 7.3 | 4.7 | 7.3 |
| BZ 18 | 23.0 | 21.9 | 19.8 | 24.5 | 31.9 | 26.1 | 8.9 | 3.2 | 12.1 |
| BZ 19 | 20.9 | 24.2 | 19.0 | 23.3 | 30.4 | 22.4 | 20.1 | 19.9 | 19.4 |
| BZ 20 | 34.5 | 8.6 | 23.9 | 32.3 | 19.7 | 13.2 | 11.1 | 4.9 | 9.2 |

a role in the lower-than-expected substitutability values. Rats that displayed a side bias in the *conc* VR 10 VR 10 condition tended to allocate more responses to that alternative, even when its requirement was subsequently increased to VR 20. In contrast, far fewer responses were allocated to the initially nonpreferred alternative when its requirement was subsequently increased to VR 20. The source of these biases is unknown; however, it is possible that their influence might dissipate over a greater number of sessions.

In terms of preference, response rates from the *conc* VR 10 VR 10 conditions for the wheel-wheel and sucrose-sucrose arrangements were not predictive of preference between sucrose and wheel running. Table 5 shows that every rat except BZ 9 took less time to make 400 responses when sucrose rather than wheel running was the reinforcer on both alternatives. Rats took 14.3 min, on average (exclusive of reinforcer and postreinforcement pause duration), to generate 400 responses with wheel running on both alternatives; with sucrose on both, it was 6.3 min. Consistent with this, every rat except BZ 9 had a higher local response rate when both alternatives produced sucrose. The mean local response rate for sucrose-sucrose ($M = 71.21$ presses/min) was more than twice the rate with wheel running on both alternatives ($M = 33.12$, presses/min), $t(11) = -5.75$, $p < .001$. For the sucrose-wheel arrangement, however, response rates and obtained reinforcers did not differ (Table 5). Specifically, on *conc* VR 10 VR

10 schedules of sucrose and wheel running, rats obtained an average of 29.2 sucrose and 29.3 wheel-running reinforcers. Mean local response rates on the sucrose and wheel-running alternatives were 45.3 and 48.4 presses/min, respectively. At the level of individual animals, seven rats obtained more sucrose reinforcers and had higher local rates on the sucrose alternative.

With respect to wheel running, rate of running varied inversely with number of opportunities to run (obtained reinforcers). For the wheel-wheel arrangement, mean wheel-running rates in the *conc* VR 10 VR 10, *conc* VR 5 VR 20, and *conc* VR 20 VR 5 conditions were 36.4, 32.6, and 33.1, revolutions/min, respectively; mean obtained reinforcers (opportunities to run) were 39.2, 86.4, and 68.5, respectively. A linear regression of wheel-running rates on obtained reinforcers produced slope, intercept, and variance accounted for values of -0.07 , 38.83 , and $.34$. For the wheel-sucrose arrangement, mean wheel-running rates in the equivalent conditions were 40.7, 49.1, and 35.3, revolutions/min; mean obtained wheel-running reinforcers were 29.3, 12.2, and 72.0. A similar regression produced slope, intercept, and variance accounted for values of $-.18$, 48.67 , and $.65$. For both the wheel-wheel and sucrose-wheel combinations, rate of running per opportunity increased as the number of obtained reinforcers decreased (slopes, $t(35) = -2.10$, $p = .04$; $t(35) = -5.04$, $p < .001$). These results suggest that changes in the

Table 5

Local response rate (lever presses/min) and time (min) to complete 400 lever presses in the concurrent VR 10 VR 10 conditions for the wheel-wheel and sucrose-sucrose combinations for each rat. Also presented are local response rate and obtained reinforcers on the sucrose and wheel running alternatives from the concurrent VR 10 VR 10 condition of the sucrose-wheel combination for each rat.

| Rat | Wheel-wheel | | Sucrose-sucrose | | Sucrose-wheel | | | |
|-------|-------------|-------|-----------------|------|---------------|-------|-------|-------|
| | Rate | Time | Rate | Time | Rate | Reinf | Rate | Reinf |
| BZ 2 | 51.30 | 7.80 | 87.52 | 4.57 | 44.1 | 23.1 | 57.2 | 35.4 |
| BZ 6 | 27.06 | 14.78 | 80.17 | 4.99 | 37.1 | 31.0 | 26.1 | 27.9 |
| BZ 7 | 37.40 | 10.69 | 40.08 | 9.98 | 32.8 | 20.3 | 54.4 | 38.0 |
| BZ 9 | 47.28 | 8.46 | 44.89 | 8.91 | 41.3 | 21.8 | 54.0 | 36.6 |
| BZ 10 | 61.37 | 6.52 | 113.95 | 3.51 | 45.3 | 34.7 | 105.8 | 23.3 |
| BZ 11 | 25.63 | 15.61 | 54.29 | 7.37 | 32.3 | 36.3 | 21.4 | 22.7 |
| BZ 12 | 17.44 | 22.94 | 81.73 | 4.89 | 49.6 | 36.2 | 32.9 | 23.1 |
| BZ 14 | 17.92 | 22.32 | 48.59 | 8.23 | 48.4 | 35.4 | 47.3 | 23.1 |
| BZ 15 | 24.39 | 16.40 | 98.28 | 4.07 | 63.9 | 42.0 | 74.5 | 15.8 |
| BZ 18 | 32.56 | 12.28 | 84.31 | 4.74 | 32.6 | 13.6 | 27.2 | 44.6 |
| BZ 19 | 38.09 | 10.50 | 78.23 | 5.11 | 86.2 | 32.9 | 58.4 | 26.4 |
| BZ 20 | 17.00 | 23.52 | 42.54 | 9.40 | 29.6 | 23.3 | 21.7 | 34.7 |

economic conditions (budgets and prices) affected the number of wheel-running reinforcers obtained, as well as the rate of wheel running per opportunity. As the number of opportunities to run increased, animals decreased the rate of running per opportunity; in contrast, as the number of opportunities decreased, the rates of running increased. Overall, the animals appear to compensate for changes in the number of wheel-running opportunities imposed by the economic constraints by adjusting their rates of running per opportunity.

Lastly, for the *conc* VR 10 VR 10 condition of the sucrose-wheel combination, the type of reinforcer obtained for the first 10 reinforcers of the session was assessed. Average percentages of sucrose reinforcers obtained for the first to the tenth reinforcers were 47, 55, 56, 57, 56, 51, 53, 53, 49, and 56. Thus, at the beginning of a session, animals were just as likely to obtain wheel running as they were to obtain sucrose. Although food deprived, these animals were not consuming and satiating on sucrose before choosing to run.

DISCUSSION

The results from Experiment 2 show that sucrose and wheel running have complex interrelationships. In terms of the economic relation, the findings suggest partial substitutability and asymmetry in the relationship—wheel running is independent of sucrose whereas sucrose functions as a partial sub-

stitute for wheel running. Previous research assessing the substitutability of food and water also showed asymmetrical relations (Allison & Mack, 1982; Rachlin & Krasnoff, 1983). Water substituted for food when rats were food deprived; however, when the rats were water deprived, the two commodities were complements (less water and food consumed). The current results also indicate that substitutability values for sucrose-sucrose were greater than for the wheel-wheel combination with both arrangements falling below the expected value for perfect substitutes. The data for changeovers show that rats have a higher tendency to switch between alternatives when the reinforcer is wheel running than when it is sucrose. The difference in switching appears to account for the lower substitutability values of the wheel-wheel arrangement relative to the sucrose-sucrose combination.

In terms of changeovers, Belke and Belliveau (2001) also observed high levels of switching for rats on concurrent VI schedules of wheel-running reinforcement, using the apparatus from the current study. Across the different schedule combinations investigated, the mean percentage of total responses that were changeover responses was 27.4%. When response allocations were corrected for changeovers by subtracting one response from each alternative for every changeover from that alternative, the difference in sensitivity between response and time allocation disappeared.

Table 6

Substitutability values, uncorrected (U) and corrected (C) for changeovers, for the sucrose-wheel, wheel-wheel, and sucrose-sucrose combinations for each rat that completed all combinations.

| Rat | Sucrose-wheel | | Wheel-wheel | | Sucrose-sucrose | |
|-------|---------------|-------|-------------|------|-----------------|------|
| | U | C | U | C | U | C |
| BZ 2 | 0.50 | 0.56 | 0.63 | 0.71 | 0.60 | 0.62 |
| BZ 6 | 0.10 | 0.11 | 0.62 | 0.71 | 0.70 | 0.73 |
| BZ 7 | 0.09 | 0.12 | 0.44 | 0.55 | 0.58 | 0.62 |
| BZ 9 | 0.00 | 0.02 | 0.26 | 0.42 | 0.35 | 0.43 |
| BZ 10 | -0.14 | -0.20 | 0.45 | 0.62 | 0.55 | 0.60 |
| BZ 11 | 0.28 | 0.34 | 0.42 | 0.53 | 0.49 | 0.55 |
| BZ 12 | 0.34 | 0.46 | 0.15 | 0.28 | 0.42 | 0.50 |
| BZ 14 | 0.08 | 0.12 | 0.15 | 0.24 | 0.33 | 0.41 |
| BZ 15 | 0.53 | 0.58 | 0.48 | 0.63 | 0.68 | 0.73 |
| BZ 18 | 0.36 | 0.45 | 0.43 | 0.59 | 0.55 | 0.58 |
| BZ 19 | -0.33 | -0.46 | 0.40 | 0.50 | 0.31 | 0.37 |
| BZ 20 | 0.48 | 0.55 | 0.55 | 0.64 | 0.59 | 0.63 |

To assess whether the difference in substitutability values between wheel running and sucrose was due to high levels of switching, the same correction was applied to the data from the present study. Response allocations were corrected by subtracting the number of changeovers for each alternative from the response allocation to that option; this correction was done for each of the ratio-schedule conditions for each rat. Reinforcer allocations were adjusted for the reduction in responses to each alternative with the constraint that the prices (responses/reinforcer) remain the same as they were for the uncorrected data. Substitutability values were then calculated for the corrected data. Table 6 shows the corrected values. Mean substitutability values for the sucrose-wheel, wheel-wheel, and sucrose-sucrose combinations based on changeover corrected data were .22, .54, and .57. Paired *t*-test comparisons showed that with the correction for switching, substitutability values for the wheel-wheel and sucrose-sucrose conditions were no longer significantly different. Correction for changeovers, however, did not alter substantially the substitutability values for the sucrose-wheel arrangement. Nor did it affect the asymmetry in economic relations between sucrose and wheel running.

It also is important to note that when the rats chose between sucrose and wheel-running reinforcers, their switching resembled the higher level observed for the wheel-wheel arrangement rather than the lower level

observed when both alternatives provided sucrose. This higher alternation in the sucrose-wheel arrangement on ratio schedules may explain the animals' switching on the modified concurrent VI VI schedules of Experiment 1; that is, by switching between alternatives, the rats were able to maintain the obtained number of wheel-running reinforcers against increasing concentrations of sucrose. On the concurrent VI schedules, a high frequency of visits to both alternatives (with sufficient responses to exceed the changeover requirements) would allow animals to obtain most, if not all, of the reinforcers set up on the schedules. In Experiment 1, the mean percentages of responses that were changeovers for the 2.5%, 7.5%, and 12.5% sucrose concentration conditions were 25.7, 21.2, and 21.0, respectively. A repeated measures ANOVA revealed no effect of concentration on the percentage of responses that were changeovers, $F(2,18) = 1.97$, ns. This insensitivity of changeovers to sucrose concentration allowed the rats to regulate their opportunities for wheel running even when the sweetness and caloric value of the sucrose alternative improved.

In addition to changeovers, Belke and Belliveau (2001) noted low response rates generated by, and long PRPs following, wheel-running reinforcement. In the present study, we also observed low response rates for wheel-running reinforcement compared to response rates for sucrose. Although not

reported in Table 3, PRPs were longer following wheel running than sucrose reinforcement. For example, in the *conc* VR 10 VR 10 condition of the sucrose-wheel arrangement, mean PRPs following wheel running and sucrose reinforcers were 14.5 and 3.7 s, respectively. Further research is required to investigate the effect of differences in response rates, PRPs, and changeovers between wheel-running and sucrose reinforcement on choice between these commodities. One possibility is that the stimulus context of the wheel chamber is integral to wheel-running reinforcement, but plays a less salient role for traditional reinforcers such as sucrose.

In terms of choice and preference, the results showed that the animals' rates of responding for wheel running and sucrose as separate reinforcers did not predict choice between these commodities. When given the opportunity to consume sucrose, animals responded at much higher rates than when given the opportunity to run; however, when offered together, animals did not prefer sucrose over wheel running. Furthermore, differences in response rates observed when the reinforcers were separately assessed disappeared when they were combined. Recently, we have taken photographs of an animal pressing a lever for opportunities to run on a wheel. The rat tended to move up the side of the braked wheel and then quickly move down and press the lever. This behavior probably was reinforced intermittently when lever pressing met the schedule requirement, released the brake, and provided the highly motivated animal with a "running start". One implication of the behavioral sequence would be to reduce the animal's response rate for wheel running. Assuming that sucrose reinforcement does not generate a similar behavioral sequence (i.e., the animal remains stationary in front of the lever while pressing), the response rate engendered by sucrose would be higher than for wheel running. This difference in topography of responding also would account for the lower asymptotic response rate generated by wheel-running reinforcement compared with sucrose (Belke, 1998). Further research is necessary to substantiate these presumed differences in topography and response rates established by contingencies of sucrose and wheel-running reinforcement arranged within the context of a running wheel.

In terms of wheel running, the results showed that animals adjust their wheel-running rates to compensate for the economic constraints on the opportunities to run. As the number of obtained reinforcers decreased, rate of running increased. Similar compensatory changes in wheel-running rate occur with changes in the duration of an opportunity to run (Belke, 1997; Belke & Hancock, 2003). As the duration of an opportunity to run decreases, running rate increases. In both cases, animals alter the level of physical activity in accord with the environmental constraints placed on wheel running. One possibility is that the changes in wheel-running rate allow food-deprived animals to defend a level of physical activity (Pierce, 2001). Another implication is that changes in wheel-running rates within opportunities to run may affect operant responding for opportunities to run (Belke, 1997; 2000). Finally, changes in wheel-running rates imply that economic constraints affect consumption in two ways—regulating the frequency of purchases (number of obtained opportunities) as well as the rate of use (wheel-running rates) within each purchase.

GENERAL DISCUSSION

A major finding of the present study is that wheel running does not substitute for sucrose on concurrent ratio schedules of reinforcement. Our result apparently contradicts Broocks et al.'s (1990) hypothesis (and observation) that hyperactivity compensates for neurotransmitter changes in NE and DA induced by semi-starvation. One possibility, resolving the differences between the studies, is that the relationship between food consumption and physical activity depends on regulation by a third variable—body weight. In an experiment by Pierce et al., (1986) using a progressive-ratio schedule of reinforcement, rats responded more for bouts of wheel running at 75% body weight than at 100% of free-feeding weight—indicating that the reinforcement value of physical activity increases with food deprivation and weight loss.

In a recent experiment by Belke (2004), the role of body weight in the regulation of the reinforcement value of both wheel running and food was clarified. Rats at low body weight initiated responding sooner, and responded faster, in the presence of stimuli signaling

upcoming opportunities to run or consume sucrose. As body weight approached free-feeding levels, the effect on behavior differed depending on the nature of the reinforcer (wheel or sucrose). Although rates of response changed to a similar degree for the wheel and food reinforcement, the probability of initiating a response for wheel running (given a signaled opportunity) decreased more with gains in body weight compared to sucrose. As weight approached *ad libitum* levels, the incentive value of a stimulus predicting food remained considerably higher than for a stimulus signaling wheel running.

In the natural habitat, animals attain free-feeding weight only when food is abundant and at these times food-related travel diminishes. As food supply is reduced by famine or drought, body weight declines driving up physical activity that in turn reduces feeding in a location or patch. Adiposity and level of energy stores, as reflected by body weight, appear to play a key role in regulating level of physical activity and food intake as food supply changes. An implication of regulation by body weight is that economic constraints on consumption may be limited by animals' long-term level of food deprivation. In other words, if body weight regulates food consumption and activity, then economic constraints may compete with body weight in affecting consumption of these two commodities. As a result, changes in economic constraints may not yield all possible bundles of these two commodities—from all sucrose with no wheel running to all wheel running with no sucrose.

In the present study, body weight was controlled and maintained at 85% of free-feeding adult weight (400 g for males, 300 g for females). Due to postsession feeding, changes in the consumption of sucrose during reinforcement periods did not translate into changes in body weight that would lower animals' consumption of wheel running. In order to investigate the effect of body weight on wheel running and food consumption, the relationship between wheel running and sucrose would need to be assessed at different body-weight levels. Future research should use concurrent ratio schedules to investigate substitutability between sucrose and wheel running when animals are maintained at 75 and 95 percent of their free-feeding weights.

Another major finding from the present study is that sucrose partially substitutes for wheel running. This finding may be relevant to the cessation of activity that occurs as food availability increases in a location or patch. Belke *et al.* (2004) showed that prefeeding an animal before a session of responding for an opportunity to wheel run produced a transient decrease in running and responding—a finding in accord with the partial substitutability of sucrose for wheel running. When prefeeding increased body weight, however, substantive and sustained decreases in running and lever pressing for running occurred. The partial substitutability of food for physical activity may be a mechanism that underlies the cessation of activity anorexia.

One limitation of our study is that the control of body weight through postsession feeding (i.e., an open economy) has implications for assessing the economic effects of food restriction. In the open economy of our experiment, the price of food has two components: the price of food during the session (earned food) and the free food supplied outside the experimental session. Let's say that the price of the earned food is X and the price of the free food is zero so the average price of food must be less than X . If free food is now restricted and more is earned during the session, some formerly free food now costs X , so the average price of food must go up. In the natural environment, there is no free food (i.e., closed economy) and depletion of a food source or patch means that animals must do more work to obtain the same amount of food and caloric content. One implication is that food restriction in everyday habitats directly affects the price of food, but the limiting of food outside the session in our experiment only indirectly altered the overall cost of food. If animals earned all of their food in the operant chamber (e.g., Collier & Johnson, 1997) then the effects of food restriction would parallel more closely the economic situation faced by foraging animals in the wild.

Extension to Activity Anorexia

With respect to the phenomenon of activity anorexia, the current results showed that when given a choice between running and eating, hungry rats did not abandon running. The contingencies of reinforcement of this study allowed the rats to respond exclusively to one

alternative—but exclusive preference did not develop. Additionally, there was no requirement that the rats run on their wheels during the reinforcement period. However, the food-deprived animals maintained a level of running while shifting more time and behavior to the sucrose alternative, obtaining a greater number of sucrose reinforcers. These findings and considerations have implications for an analysis of activity anorexia based behavior principles and considerations of evolution and natural selection (Epling & Pierce, 1991; Epling et al., 1983; Pierce, 2001).

During times of famine, there would be a net negative energy balance between foraging for small, less-preferred, and difficult-to-obtain food items and traveling to a more-abundant food source (see marginal value theorem (MVT), Charnov, 1976; qualitative predictions of MVT are well supported by research; quantitative predictions have been less accurate, Nonacs, 2001). Reduction of food supply (increased price) would have increased locomotion or travel mostly through its local effects on body weight and energy stores. Longer-term reduction of body weight would have instigated and maintained food-related travel of foraging animals, or the wheel running of our experimental rats (Belke et al., 2004; Pierce, 2001). In everyday niches, increasing contact with food (new patch) would have resulted in reduction of travel, an increase in body weight, and termination of the food-related trek. The partial substitutability of sucrose for wheel running in the present study reflects one aspect of two energy-balance processes; the initiation and maintenance of travel induced by loss of body weight and energy stores (wheel running does not substitute for food) and the termination of locomotion as food supply increases (food does substitute for wheel running).

In the present study, rats maintained their level of wheel running (Collier & Hirsch, 1971; see also Sherwin, 1998 for similar behavior in mice) even as the quality (concentration of sucrose) and frequency (obtained sucrose reinforcers) of food improved—presumably, because the nutritional changes did not alleviate deprivation or increase body weight. At the same time, the rats showed sensitivity to the changes in quality and frequency of food in their environment (Redhead & Tyler, 1988). Although the schedules of reinforce-

ment differed for the two manipulations—concurrent modified VI VI schedules for the concentration manipulation and concurrent VR VR schedules for the frequency manipulations—frequency had a greater effect on the distribution of behavior than did concentration.

Sensitivity to the frequency or density of food in a location may be one way that animals eventually stop a food-related trek (Johnson, Tribblehorn, & Collier, 1995). In natural habitats, food quality and quantity do not necessarily occur together—high quality food (high caloric value) can be either prevalent or sparse. Unless food items occur at high frequency, improvement in body weight and energy reserves would not be sustained and the search for food should continue. The general implication is that density is a better predictor of food availability than quality when animals are on an extended food-related trek.

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APPENDIX A

Mean responses, time (in s), reinforcers, changeovers (CO), and revolutions for the wheel (W) and sucrose (S) alternatives for each sucrose concentration for each rat. The schedule of reinforcement was a modified concurrent VI 30-s VI 30-s schedule. Sessions (Sess) to stability for each schedule also are provided. Base refers to the baseline condition in which both alternatives produced the opportunity to run for 30 s. This condition occurred prior to changing one of the alternatives to sucrose reinforcement. The alternative that was changed to sucrose reinforcement is listed under "S".

| Rat | Conc | Sess | Responses | | Time | | Reinforcers | | CO | | Revs |
|-------|------|------|-----------|--------|--------|--------|-------------|------|-------|-------|--------|
| | | | W | S | W | S | W | S | W | S | |
| ID 1 | 2.5 | 20 | 529.8 | 218.8 | 1036.7 | 309.6 | 36.2 | 28.8 | 101.2 | 100.8 | 841.0 |
| | 7.5 | 28 | 619.8 | 534.4 | 566.1 | 767.8 | 34.4 | 37.8 | 186.0 | 186.2 | 806.6 |
| | 12.5 | 36 | 506.4 | 603.8 | 636.3 | 849.1 | 36.2 | 41.4 | 159.6 | 160.0 | 745.4 |
| | Base | | 287.6 | 254.6 | 584.3 | 398.0 | 22.0 | 23.2 | 87.2 | 86.6 | 1065.0 |
| ID 6 | 2.5 | 38 | 389.4 | 220.4 | 679.3 | 472.8 | 31.8 | 23.8 | 73.4 | 73.2 | 642.0 |
| | 7.5 | 38 | 370.8 | 388.0 | 532.1 | 708.9 | 32.2 | 31.6 | 103.8 | 103.6 | 649.4 |
| | 12.5 | 22 | 302.0 | 424.6 | 453.0 | 860.8 | 30.8 | 34.8 | 113.4 | 113.0 | 571.2 |
| | Base | | 218.8 | 148.2 | 493.1 | 355.2 | 20.6 | 17.8 | 60.2 | 60.0 | 670.8 |
| ID 12 | 2.5 | 37 | 366.8 | 399.2 | 614.0 | 523.4 | 27.6 | 28.4 | 74.6 | 74.0 | 580.6 |
| | 7.5 | 36 | 223.2 | 1360.8 | 186.2 | 1652.7 | 27.6 | 56.2 | 94.8 | 94.0 | 594.0 |
| | 12.5 | 21 | 134.6 | 2839.0 | 115.8 | 1983.9 | 19.2 | 70.2 | 51.2 | 51.0 | 449.2 |
| | Base | | 184.8 | 132.8 | 427.2 | 234.0 | 13.8 | 14.0 | 37.2 | 37.2 | 561.2 |
| ID 17 | 2.5 | 40 | 152.2 | 131.0 | 470.1 | 633.0 | 19.6 | 20.2 | 40.0 | 40.0 | 319.4 |
| | 7.5 | 40 | 91.8 | 628.2 | 140.3 | 1711.3 | 17.8 | 51.0 | 47.2 | 47.4 | 309.8 |
| | 12.5 | 40 | 99.8 | 679.6 | 153.5 | 1839.8 | 19.0 | 61.6 | 40.4 | 41.0 | 373.6 |
| | Base | | 94.2 | 99.6 | 120.9 | 511.5 | 9.0 | 12.4 | 36.0 | 36.2 | 372.2 |
| ID 19 | 2.5 | 40 | 125.2 | 131.4 | 432.9 | 973.2 | 18.2 | 20.0 | 49.0 | 49.6 | 200.8 |
| | 7.5 | 31 | 90.0 | 473.8 | 202.9 | 1621.4 | 15.8 | 45.6 | 48.6 | 48.6 | 178.8 |
| | 12.5 | 24 | 187.8 | 546.0 | 323.8 | 1514.3 | 28.0 | 50.6 | 91.0 | 91.4 | 354.4 |
| | Base | | 210.0 | 127.2 | 463.1 | 208.5 | 13.6 | 11.0 | 81.4 | 81.4 | 302.8 |
| KC 4 | 2.5 | 26 | 382.2 | 94.8 | 744.1 | 213.0 | 30.0 | 13.6 | 63.8 | 63.4 | 468.4 |
| | 7.5 | 40 | 221.8 | 64.2 | 718.9 | 211.6 | 26.0 | 12.4 | 29.6 | 29.4 | 411.6 |
| | 12.5 | 39 | 151.8 | 190.6 | 382.2 | 792.4 | 25.6 | 28.0 | 52.4 | 52.2 | 355.2 |
| | Base | | 132.4 | 90.2 | 454.4 | 254.0 | 18.0 | 13.6 | 39.4 | 39.0 | 467.0 |
| KC 8 | 2.5 | 39 | 175.8 | 74.4 | 592.3 | 127.9 | 19.6 | 13.6 | 29.8 | 29.8 | 276.4 |
| | 7.5 | 37 | 233.8 | 104.8 | 620.1 | 166.5 | 20.2 | 16.8 | 47.2 | 47.2 | 331.6 |
| | 12.5 | 40 | 184.4 | 183.8 | 525.5 | 310.1 | 16.8 | 18.6 | 45.6 | 46.0 | 243.0 |
| | Base | | 140.2 | 92.8 | 410.9 | 152.5 | 12.8 | 10.8 | 28.2 | 28.4 | 357.6 |
| KC 9 | 2.5 | 40 | 210.8 | 257.4 | 400.9 | 367.0 | 21.2 | 21.2 | 65.6 | 64.8 | 335.4 |
| | 7.5 | 39 | 183.8 | 546.6 | 228.3 | 1017.8 | 23.6 | 36.4 | 74.2 | 73.6 | 384.2 |
| | 12.5 | 40 | 162.0 | 866.2 | 171.2 | 1346.1 | 24.4 | 46.8 | 63.8 | 63.0 | 378.0 |
| | Base | | 190.0 | 141.2 | 268.7 | 269.6 | 15.4 | 14.8 | 52.2 | 52.6 | 453.4 |
| KC 15 | 2.5 | 40 | 114.0 | 542.8 | 157.1 | 1837.0 | 20.8 | 61.2 | 35.6 | 35.6 | 211.8 |
| | 7.5 | 39 | 67.2 | 911.8 | 67.4 | 2235.8 | 19.6 | 75.4 | 29.4 | 29.2 | 242.2 |
| | 12.5 | 40 | 101.0 | 798.6 | 110.3 | 2058.8 | 19.4 | 65.0 | 34.8 | 35.4 | 250.6 |
| | Base | | 129.8 | 101.6 | 323.9 | 451.4 | 12.6 | 12.6 | 39.8 | 39.6 | 313.6 |
| KC 17 | 2.5 | 40 | 382.6 | 154.4 | 715.0 | 367.6 | 33.2 | 22.2 | 90.4 | 90.6 | 601.2 |
| | 7.5 | 21 | 426.2 | 173.6 | 702.4 | 578.3 | 35.2 | 23.0 | 106.4 | 106.0 | 672.0 |
| | 12.5 | 27 | 312.4 | 224.4 | 647.3 | 588.1 | 34.4 | 27.6 | 82.4 | 82.2 | 664.8 |
| | Base | | 281.2 | 145.0 | 485.3 | 332.2 | 23.2 | 18.2 | 70.0 | 69.6 | 778.6 |

APPENDIX B

Mean responses, time (in s), reinforcers, and revolutions on the left (L) and right (R) alternatives from the nine sessions that met the stability criteria for each concurrent ratio schedule for the sucrose-wheel, wheel-wheel, and sucrose-sucrose reinforcer combinations for each rat. Time spent lever pressing is exclusive of reinforcer and postreinforcement pause durations. Average total changeovers (CO), average session time in minutes (ST), and number of sessions to stability (SS) also are provided.

| Rat | Schedule | | Responses | | Time | | Reinforcers | | CO | Revolutions | | ST | SS | | |
|-------|----------|---|-----------|-----|------|-----|-------------|------|-----|-------------|-----|------|------|-----|----|
| | L | R | L | R | L | R | L | R | | L | R | | | | |
| BZ 2 | S | W | 10 | 10 | 237 | 363 | 328 | 395 | 23 | 35 | 114 | 0 | 808 | 39 | 30 |
| | S | W | 20 | 5 | 61 | 578 | 402 | 2306 | 2 | 115 | 66 | 0 | 1983 | 154 | 20 |
| | S | W | 5 | 20 | 563 | 261 | 329 | 418 | 112 | 13 | 90 | 0 | 346 | 30 | 29 |
| | W | W | 10 | 10 | 26 | 374 | 40 | 428 | 2 | 37 | 23 | 43 | 765 | 41 | 20 |
| | W | W | 20 | 5 | 9 | 222 | 21 | 271 | 0 | 44 | 14 | 7 | 1027 | 39 | 28 |
| | W | W | 5 | 20 | 668 | 82 | 1702 | 557 | 133 | 4 | 100 | 2522 | 68 | 174 | 26 |
| | S | S | 10 | 10 | 293 | 107 | 178 | 96 | 29 | 10 | 27 | 0 | 0 | 7 | 36 |
| | S | S | 20 | 5 | 95 | 534 | 85 | 274 | 4 | 106 | 43 | 0 | 0 | 13 | 25 |
| S | S | 5 | 20 | 328 | 19 | 149 | 23 | 65 | 1 | 11 | 0 | 0 | 7 | 23 | |
| BZ 6 | W | S | 10 | 10 | 282 | 318 | 654 | 526 | 28 | 31 | 229 | 714 | 0 | 47 | 36 |
| | W | S | 20 | 5 | 195 | 518 | 347 | 657 | 9 | 104 | 169 | 305 | 0 | 33 | 27 |
| | W | S | 5 | 20 | 256 | 504 | 547 | 914 | 51 | 24 | 226 | 1209 | 0 | 76 | 21 |
| | W | W | 10 | 10 | 45 | 355 | 133 | 754 | 4 | 36 | 56 | 77 | 852 | 53 | 42 |
| | W | W | 20 | 5 | 12 | 243 | 34 | 310 | 1 | 48 | 19 | 17 | 1035 | 49 | 21 |
| | W | W | 5 | 20 | 525 | 216 | 1785 | 782 | 105 | 10 | 227 | 1953 | 164 | 153 | 24 |
| | S | S | 10 | 10 | 50 | 350 | 71 | 228 | 4 | 34 | 44 | 0 | 0 | 7 | 20 |
| | S | S | 20 | 5 | 4 | 248 | 4 | 116 | 0 | 49 | 6 | 0 | 0 | 5 | 21 |
| S | S | 5 | 20 | 600 | 101 | 496 | 117 | 119 | 4 | 68 | 0 | 0 | 18 | 33 | |
| BZ 7 | W | S | 10 | 10 | 391 | 209 | 460 | 395 | 38 | 20 | 180 | 744 | 0 | 47 | 22 |
| | W | S | 20 | 5 | 430 | 432 | 431 | 362 | 21 | 86 | 165 | 457 | 0 | 37 | 24 |
| | W | S | 5 | 20 | 342 | 254 | 554 | 464 | 68 | 12 | 135 | 1204 | 0 | 78 | 30 |
| | W | W | 10 | 10 | 312 | 88 | 381 | 261 | 30 | 8 | 96 | 541 | 118 | 42 | 22 |
| | W | W | 20 | 5 | 141 | 499 | 346 | 1753 | 6 | 100 | 173 | 116 | 1745 | 133 | 25 |
| | W | W | 5 | 20 | 220 | 82 | 966 | 293 | 43 | 4 | 81 | 791 | 57 | 73 | 23 |
| | S | S | 10 | 10 | 243 | 157 | 367 | 232 | 24 | 15 | 72 | 0 | 0 | 12 | 20 |
| | S | S | 20 | 5 | 43 | 503 | 72 | 346 | 3 | 101 | 34 | 0 | 0 | 16 | 21 |
| S | S | 5 | 20 | 340 | 76 | 188 | 109 | 67 | 3 | 52 | 0 | 0 | 10 | 24 | |
| BZ 9 | S | W | 10 | 10 | 227 | 373 | 337 | 420 | 22 | 37 | 229 | 0 | 767 | 39 | 22 |
| | S | W | 20 | 5 | 271 | 348 | 646 | 427 | 13 | 69 | 276 | 0 | 1224 | 66 | 20 |
| | S | W | 5 | 20 | 367 | 474 | 484 | 493 | 73 | 23 | 289 | 0 | 583 | 36 | 25 |
| | W | W | 10 | 10 | 123 | 277 | 198 | 309 | 12 | 28 | 152 | 236 | 534 | 36 | 24 |
| | W | W | 20 | 5 | 118 | 267 | 328 | 607 | 6 | 52 | 172 | 89 | 871 | 58 | 24 |
| | W | W | 5 | 20 | 342 | 276 | 943 | 759 | 69 | 13 | 279 | 1140 | 200 | 88 | 21 |
| | S | S | 10 | 10 | 32 | 368 | 100 | 435 | 3 | 35 | 52 | 0 | 0 | 14 | 21 |
| | S | S | 20 | 5 | 33 | 207 | 53 | 95 | 2 | 41 | 39 | 0 | 0 | 6 | 20 |
| S | S | 5 | 20 | 300 | 420 | 457 | 369 | 60 | 20 | 157 | 0 | 0 | 21 | 35 | |
| BZ 10 | S | W | 10 | 10 | 355 | 245 | 507 | 156 | 35 | 23 | 94 | 0 | 488 | 33 | 21 |
| | S | W | 20 | 5 | 580 | 231 | 814 | 118 | 29 | 46 | 137 | 0 | 795 | 51 | 23 |
| | S | W | 5 | 20 | 412 | 228 | 435 | 184 | 82 | 11 | 82 | 0 | 263 | 29 | 25 |
| | W | W | 10 | 10 | 87 | 313 | 145 | 246 | 8 | 31 | 94 | 129 | 556 | 43 | 44 |
| | W | W | 20 | 5 | 43 | 267 | 135 | 494 | 2 | 53 | 69 | 36 | 912 | 63 | 21 |
| | W | W | 5 | 20 | 457 | 206 | 2003 | 249 | 91 | 9 | 159 | 1591 | 168 | 141 | 23 |
| | S | S | 10 | 10 | 78 | 322 | 68 | 142 | 7 | 33 | 39 | 0 | 0 | 17 | 24 |
| | S | S | 20 | 5 | 7 | 301 | 8 | 98 | 0 | 60 | 8 | 0 | 0 | 5 | 20 |
| S | S | 5 | 20 | 513 | 176 | 189 | 87 | 102 | 9 | 45 | 0 | 0 | 13 | 46 | |

APPENDIX B

(Continued)

| Rat | L | R | Schedule | | Responses | | Time | | Reinforcers | | CO | Revolutions | | ST | SS |
|-------|---|---|----------|----|-----------|-----|------|------|-------------|-----|-----|-------------|------|-----|----|
| | | | L | R | L | R | L | R | L | R | | L | R | | |
| BZ 11 | W | S | 10 | 10 | 231 | 369 | 700 | 787 | 23 | 36 | 104 | 381 | 0 | 48 | 28 |
| | W | S | 20 | 5 | 136 | 500 | 507 | 483 | 6 | 100 | 98 | 145 | 0 | 29 | 22 |
| | W | S | 5 | 20 | 388 | 452 | 1328 | 620 | 77 | 21 | 136 | 1151 | 0 | 106 | 25 |
| | W | W | 10 | 10 | 217 | 183 | 597 | 339 | 23 | 18 | 123 | 339 | 272 | 48 | 36 |
| | W | W | 20 | 5 | 131 | 411 | 523 | 802 | 5 | 82 | 170 | 75 | 1105 | 109 | 23 |
| | W | W | 5 | 20 | 352 | 121 | 1252 | 370 | 71 | 5 | 118 | 963 | 69 | 100 | 22 |
| | S | S | 10 | 10 | 247 | 153 | 314 | 128 | 24 | 14 | 95 | 0 | 0 | 10 | 26 |
| | S | S | 20 | 5 | 170 | 387 | 193 | 284 | 8 | 77 | 143 | 0 | 0 | 14 | 20 |
| | S | S | 5 | 20 | 350 | 54 | 242 | 37 | 70 | 3 | 42 | 0 | 0 | 9 | 20 |
| BZ 12 | S | W | 10 | 10 | 364 | 236 | 449 | 440 | 36 | 23 | 242 | 0 | 556 | 35 | 23 |
| | S | W | 20 | 5 | 442 | 398 | 625 | 843 | 21 | 78 | 452 | 0 | 1499 | 76 | 22 |
| | S | W | 5 | 20 | 537 | 106 | 535 | 397 | 107 | 4 | 151 | 0 | 122 | 32 | 27 |
| | W | W | 10 | 10 | 268 | 132 | 785 | 591 | 26 | 12 | 176 | 550 | 234 | 54 | 20 |
| | W | W | 20 | 5 | 292 | 298 | 502 | 532 | 14 | 60 | 304 | 285 | 1089 | 68 | 21 |
| | W | W | 5 | 20 | 236 | 142 | 520 | 465 | 47 | 6 | 197 | 931 | 101 | 51 | 35 |
| | S | S | 10 | 10 | 304 | 96 | 200 | 94 | 30 | 9 | 121 | 0 | 0 | 9 | 21 |
| | S | S | 20 | 5 | 173 | 466 | 105 | 275 | 7 | 93 | 86 | 0 | 0 | 15 | 33 |
| | S | S | 5 | 20 | 259 | 65 | 141 | 58 | 52 | 2 | 71 | 0 | 0 | 9 | 20 |
| BZ 14 | S | W | 10 | 10 | 364 | 236 | 464 | 307 | 35 | 23 | 228 | 0 | 436 | 30 | 23 |
| | S | W | 20 | 5 | 536 | 288 | 895 | 494 | 26 | 57 | 319 | 0 | 1179 | 64 | 23 |
| | S | W | 5 | 20 | 448 | 191 | 509 | 244 | 88 | 9 | 221 | 0 | 201 | 27 | 20 |
| | W | W | 10 | 10 | 253 | 147 | 964 | 375 | 24 | 15 | 161 | 442 | 289 | 51 | 25 |
| | W | W | 20 | 5 | 273 | 286 | 1201 | 1801 | 15 | 57 | 258 | 210 | 932 | 108 | 21 |
| | W | W | 5 | 20 | 257 | 162 | 1162 | 982 | 51 | 7 | 181 | 797 | 126 | 78 | 21 |
| | S | S | 10 | 10 | 167 | 233 | 196 | 297 | 15 | 23 | 128 | 0 | 0 | 12 | 25 |
| | S | S | 20 | 5 | 149 | 272 | 132 | 280 | 7 | 54 | 124 | 0 | 0 | 13 | 22 |
| | S | S | 5 | 20 | 373 | 162 | 267 | 161 | 74 | 7 | 128 | 0 | 0 | 14 | 21 |
| BZ 15 | S | W | 10 | 10 | 431 | 169 | 416 | 141 | 42 | 16 | 198 | 0 | 295 | 23 | 25 |
| | S | W | 20 | 5 | 599 | 320 | 1052 | 383 | 29 | 64 | 286 | 0 | 989 | 68 | 21 |
| | S | W | 5 | 20 | 512 | 14 | 240 | 23 | 103 | 1 | 17 | 0 | 21 | 12 | 25 |
| | W | W | 10 | 10 | 190 | 210 | 483 | 501 | 19 | 22 | 173 | 280 | 337 | 45 | 21 |
| | W | W | 20 | 5 | 126 | 350 | 389 | 701 | 6 | 70 | 179 | 67 | 852 | 81 | 22 |
| | W | W | 5 | 20 | 457 | 90 | 675 | 314 | 91 | 4 | 134 | 1155 | 49 | 92 | 21 |
| | S | S | 10 | 10 | 373 | 27 | 198 | 46 | 37 | 2 | 29 | 0 | 0 | 8 | 22 |
| | S | S | 20 | 5 | 69 | 674 | 37 | 336 | 4 | 135 | 54 | 0 | 0 | 17 | 23 |
| | S | S | 5 | 20 | 214 | 11 | 68 | 11 | 44 | 1 | 11 | 0 | 0 | 5 | 22 |
| BZ 18 | W | S | 10 | 10 | 455 | 145 | 1063 | 278 | 45 | 14 | 138 | 864 | 0 | 63 | 41 |
| | W | S | 20 | 5 | 491 | 469 | 1050 | 648 | 25 | 93 | 210 | 588 | 0 | 57 | 21 |
| | W | S | 5 | 20 | 404 | 91 | 1308 | 406 | 81 | 5 | 98 | 1358 | 0 | 95 | 26 |
| | W | W | 10 | 10 | 303 | 97 | 573 | 165 | 30 | 9 | 98 | 487 | 147 | 43 | 21 |
| | W | W | 20 | 5 | 204 | 435 | 897 | 1872 | 9 | 87 | 204 | 147 | 1286 | 127 | 22 |
| | W | W | 5 | 20 | 281 | 53 | 652 | 100 | 56 | 2 | 87 | 902 | 30 | 54 | 26 |
| | S | S | 10 | 10 | 184 | 216 | 106 | 179 | 18 | 21 | 36 | 0 | 0 | 9 | 27 |
| | S | S | 20 | 5 | 18 | 450 | 35 | 319 | 1 | 90 | 15 | 0 | 0 | 14 | 21 |
| | S | S | 5 | 20 | 333 | 171 | 232 | 218 | 66 | 8 | 61 | 0 | 0 | 14 | 21 |
| BZ 19 | S | W | 10 | 10 | 334 | 266 | 237 | 280 | 33 | 26 | 125 | 0 | 467 | 30 | 24 |
| | S | W | 20 | 5 | 510 | 280 | 512 | 464 | 25 | 56 | 150 | 0 | 896 | 64 | 23 |
| | S | W | 5 | 20 | 328 | 365 | 186 | 319 | 65 | 17 | 168 | 0 | 383 | 25 | 20 |
| | W | W | 10 | 10 | 170 | 230 | 235 | 395 | 16 | 22 | 93 | 267 | 396 | 40 | 24 |
| | W | W | 20 | 5 | 88 | 345 | 248 | 521 | 3 | 68 | 97 | 38 | 878 | 69 | 30 |
| | W | W | 5 | 20 | 362 | 161 | 599 | 416 | 72 | 7 | 159 | 804 | 87 | 85 | 25 |
| | S | S | 10 | 10 | 298 | 102 | 202 | 105 | 29 | 10 | 80 | 0 | 0 | 9 | 21 |
| | S | S | 20 | 5 | 279 | 351 | 229 | 291 | 13 | 70 | 122 | 0 | 0 | 16 | 24 |
| | S | S | 5 | 20 | 255 | 83 | 245 | 104 | 51 | 3 | 67 | 0 | 0 | 12 | 24 |

APPENDIX B

(Continued)

| Rat | L | R | Schedule | | Responses | | Time | | Reinforcers | | CO | Revolutions | | ST | SS |
|-------|---|---|----------|----|-----------|-----|------|------|-------------|-----|-----|-------------|------|-----|----|
| | | | L | R | L | R | L | R | L | R | | L | R | | |
| BZ 20 | W | S | 10 | 10 | 356 | 244 | 1039 | 530 | 35 | 23 | 207 | 650 | 0 | 55 | 26 |
| | W | S | 20 | 5 | 148 | 663 | 567 | 682 | 7 | 132 | 70 | 149 | 0 | 35 | 33 |
| | W | S | 5 | 20 | 508 | 132 | 1642 | 489 | 101 | 6 | 153 | 1542 | 0 | 127 | 20 |
| | W | W | 10 | 10 | 248 | 152 | 899 | 513 | 24 | 15 | 129 | 419 | 258 | 54 | 32 |
| | W | W | 20 | 5 | 103 | 450 | 1046 | 2122 | 4 | 90 | 109 | 67 | 1442 | 152 | 37 |
| | W | W | 5 | 20 | 374 | 38 | 1956 | 448 | 74 | 2 | 54 | 1158 | 25 | 118 | 23 |
| | S | S | 10 | 10 | 89 | 311 | 240 | 324 | 8 | 31 | 44 | 0 | 0 | 13 | 25 |
| | S | S | 20 | 5 | 16 | 295 | 24 | 209 | 1 | 59 | 15 | 0 | 0 | 9 | 33 |
| | S | S | 5 | 20 | 539 | 112 | 538 | 139 | 107 | 6 | 60 | 0 | 0 | 21 | 20 |
| BZ 1 | W | S | 10 | 10 | 386 | 214 | 566 | 268 | 38 | 21 | 107 | 757 | 0 | 49 | 72 |
| | W | S | 20 | 5 | 269 | 598 | 1133 | 2320 | 13 | 119 | 179 | 252 | 0 | 88 | 32 |
| | W | S | 5 | 20 | 260 | 351 | 528 | 853 | 52 | 17 | 162 | 860 | 0 | 64 | 42 |
| | W | W | 10 | 10 | 39 | 361 | 176 | 1173 | 3 | 36 | 66 | 47 | 512 | 58 | 30 |
| | W | W | 5 | 20 | 520 | 208 | 1329 | 554 | 104 | 10 | 270 | 1558 | 156 | 130 | 39 |
| BZ 3 | W | S | 10 | 10 | 192 | 408 | 230 | 324 | 19 | 40 | 117 | 313 | 0 | 29 | 50 |
| | W | S | 20 | 5 | 457 | 123 | 917 | 285 | 24 | 23 | 155 | 375 | 0 | 43 | 34 |
| | W | S | 5 | 20 | 820 | 73 | 5689 | 260 | 163 | 3 | 137 | 1936 | 0 | 284 | 35 |
| | W | W | 10 | 10 | 371 | 29 | 775 | 50 | 36 | 3 | 53 | 538 | 41 | 49 | 20 |
| BZ 8 | S | W | 10 | 10 | 130 | 470 | 129 | 487 | 12 | 46 | 173 | 0 | 954 | 44 | 22 |
| | S | W | 20 | 5 | 151 | 317 | 183 | 433 | 6 | 64 | 222 | 0 | 1260 | 53 | 23 |
| | S | W | 5 | 20 | 393 | 592 | 584 | 1757 | 78 | 29 | 462 | 0 | 741 | 69 | 24 |
| | W | W | 10 | 10 | 139 | 261 | 237 | 566 | 13 | 25 | 175 | 248 | 458 | 47 | 23 |
| | W | W | 20 | 5 | 120 | 272 | 213 | 292 | 5 | 54 | 119 | 61 | 636 | 70 | 20 |
| | W | W | 5 | 20 | 353 | 208 | 437 | 372 | 70 | 10 | 202 | 985 | 148 | 93 | 23 |
| | S | S | 10 | 10 | 58 | 342 | 214 | 596 | 5 | 33 | 57 | 0 | 0 | 18 | 28 |